

VII. *On the Structure of the Palaeozoic Seed Lagenostoma Lomaxi, with a Statement of the Evidence upon which it is referred to Lyginodendron.*

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[PLATES 4-10.]

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INTRODUCTION.

IN a note communicated to the Royal Society in May, 1903,* it was stated that a re-examination of the Palaeozoic seeds, placed by WILLIAMSON in his genus

* 'Roy. Soc. Proc.,' vol. 71, p. 477.

Lagenostoma, had revealed unexpected points of agreement between the structure of the envelopes of certain of these seeds on the one hand and that of the vegetative organs of *Lyginodendron* on the other, and the conclusion was drawn that the seed *Lagenostoma Lomaxi* could have belonged to no other plant than *Lyginodendron*.

In the present paper it is proposed to give a full statement of the evidence upon which that conclusion is based, to describe the seed in detail, and to consider the bearing of the discovery upon the question of the relations of the Ferns and Gymnosperms.

Two species of *Lagenostoma* (*L. ovoides* and *L. physoides*) were described by WILLIAMSON in his eighth memoir "On the Organisation of the Fossil Plants of the Coal Measures";* a third species which he named in his MS. catalogue, *L. Lomaxi*, after its discoverer, was left undescribed by him.

This seed (*L. Lomaxi*) is occasionally found attached to its pedicel, and is further remarkable as compared with other members of the genus in being found enclosed in an envelope or cupule springing from the pedicel just below the base of the seed and extending above the micropyle, at least in young specimens. The cupule appears to have been ribbed below, and deeply lobed in its upper part; in form it may be roughly compared to the husk of a hazel nut, of course on a very small scale.†

The pedicel and cupule bear numerous capitate glands, which, though in a state of disorganisation, have been found to offer the closest agreement in size, form, and structure, with the glands which occur on the vegetative organs of *Lyginodendron Oldhamium*, and which are especially abundant in the particular form of that plant found in association with *Lagenostoma Lomaxi*.

The reference of the seed to *Lyginodendron* is primarily based on this agreement in gland structure, but as the sequel shows, a comparison of the detailed anatomical structure of the cupule and pedicel further supports the attribution.

In the present paper we deal in successive sections: first, with the structure of the seed and with its pollination; then follows the description of the cupule and stalk, and a comparison of their structure with that of the vegetative organs of *Lyginodendron*; this includes a statement of the evidence on which we base the reference of the seed. Finally, there are sections dealing with the position of the seed on the plant, with the morphology of the seed and cupule, and with the systematic position of the genus.

THE SEED.

The seeds which have come under our observation fall under three categories. First, there are the full-sized specimens with dimensions averaging $5\frac{1}{2} \times 4\frac{1}{2}$ millims.;

* 'Phil Trans.,' vol. 167, p. 233, figs. 53-75 and 77-79, 1877.

† The photograph on p. 217 represents a restoration in wax of one of the smaller seeds, enclosed in its cupule. The model was prepared for the authors by Mr. H. E. H. SMEDLEY. The ripe nut of *Corylus*

these form the great majority. Then there are occasional smaller seeds, which, though immature in some respects, are from the appearance of their membranes and state of preservation to be regarded rather as undersized abortive seeds than as real ovular stages, that is to say, like little acorns that prematurely fall, they have reached their full limits of development. Only four seeds of this kind have passed through our hands, and of these, two which are cut across the apex lack the enveloping cupule.

Finally, there is a solitary specimen of a small seed enclosed in the cupule, which, from the peculiarity of its preservation, has considerable claim to rank as a real ovule, an immature stage, that is, possessing capacity for further development.

In the course of this memoir we enumerate all the more important specimens of *Lagenostoma Lomaxi* and of its stalk and cupule, which have been consulted in the course of the investigation. In this connection our thanks are due to Miss M. BENSON of the Royal Holloway College, to Professor C. E. BERTRAND of the University of Lille, to Mr. R. KIDSTON, F.R.S., and to Professors F. E. WEISS and I. BAYLEY BALFOUR, F.R.S., all of whom have freely placed at our disposition fossil slides in their custody or possession.

The specimens upon which our description of the full-grown seed is based are as follows:—

- * WILLIAMSON Collection, 1915, M. } Series of three transverse sections from
- * " " 1915, O. } the same seed.
- * SCOTT Collection, 236 }
- U. C. L. Collection, R. 6, a } Series of three transverse sections from
- * " " R. 6, b } the same seed.
- * " " R. 6, c }
- U. C. L. Collection, R. 7, a } Series of two transverse oblique sections
- * " " R. 7, b } from the same seed.
- * U. C. L. Collection, R. 8, a } Series of two transverse sections from
- * " " R. 8, b } the same seed.
- U. C. L. Collection, R. 9, a } Series of three transverse sections of the
- " " R. 9, b } same seed.
- * " " R. 9, c }
- * Collection of Botanical Dept., Univ. of Lille, 1110 } Series of three oblique sections from the
- * " " " 1108 } same seed.
- " " " 1109 }
- WILLIAMSON Collection, 1931 } Series of two oblique sections through
- * KIDSTON Collection, 260 } three seeds. The central seed of the three shows a forking bundle.

Colurna, L., enclosed in its glandular husk, may be cited as affording a remarkably accurate model of our seed in its cupule, so far as the form and general relations of the parts are concerned.

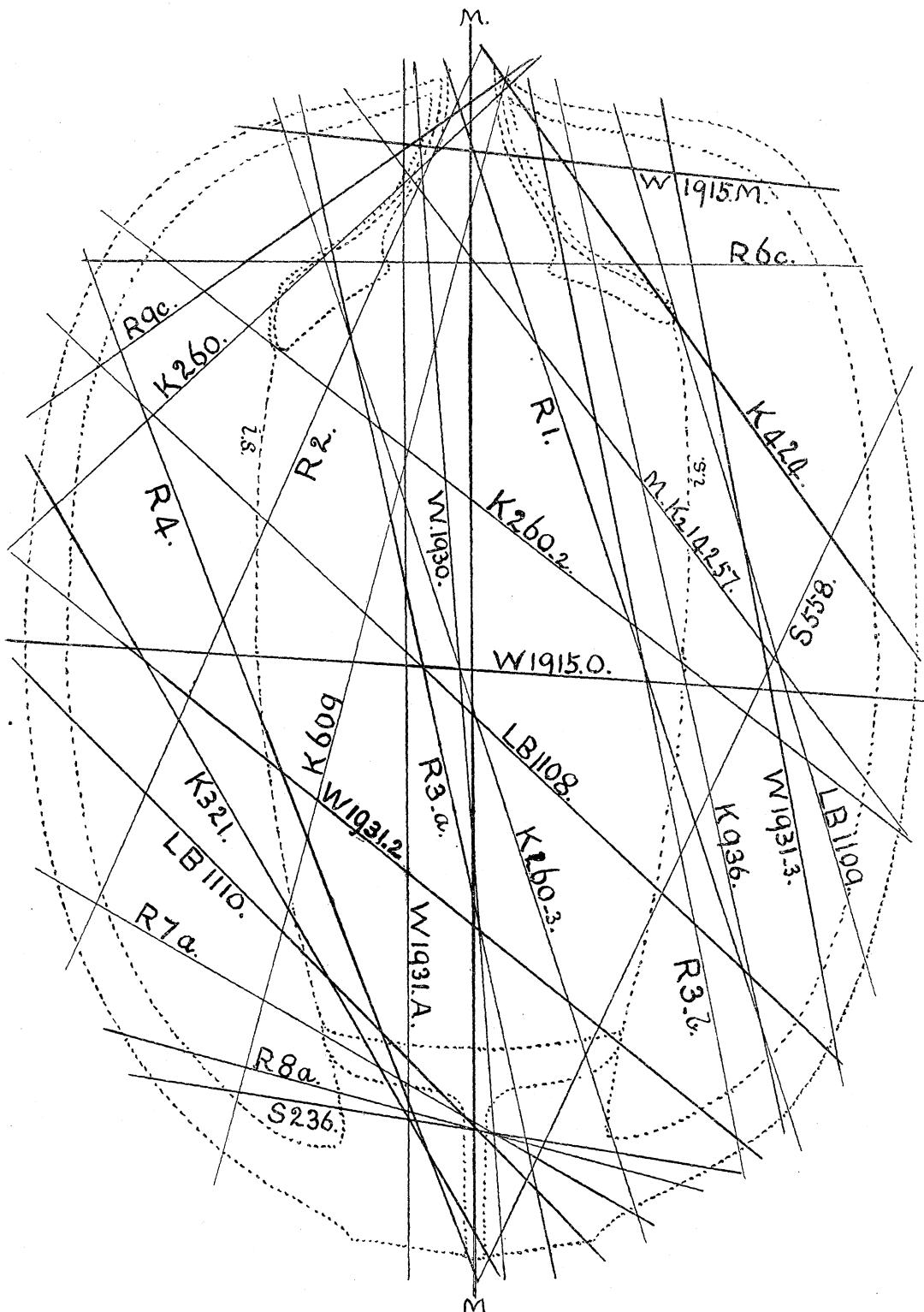
KIDSTON Collection, 321	Series of two oblique sections through
* " " 424	the same seed.
WILLIAMSON Collection, 1915 G . . .	Series of two oblique sections through
" " 1915 R	the same seed.
* U. C. L. Collection, R. 3, a	Series of two longitudinal sections
" " R. 3, b	through the same seed.
* WILLIAMSON Collection, 1930	Longitudinal section.
" " 1931, A	" "
* U. C. L. Collection, R. 1	Longitudinal section, showing pollen-chamber.
* " " R. 2	Longitudinal section, showing pollen-chamber.
* SCOTT Collection, 558	Longitudinal section, showing attachment to pedicel.
* U. C. L. Collection, R. 4	Longitudinal section, showing base.
* Manchester Museum Collection, K ₂ 14257.	Oblique section, showing pollen-chamber.
KIDSTON Collection, 609	Longitudinal section, showing pollen-chamber.
U. C. L. Collection, R. 10	Oblique section of canopy.
KIDSTON Collection, 936	Longitudinal section.
" " 937	" "

The preparations preceded by a * are figured in the present paper.

The Full-Sized Seed.

Although the sections of full-sized seeds examined have been plentiful, not one is a truly median longitudinal section. Very few approach the median plane so nearly as to traverse both the pollen-chamber and the scar at the chalaza where the seed was attached. The majority of "longitudinal sections" cut the median plane by 15° or more, so that the real relations of a median section have been obtained by a process of building up oblique sections of various sorts. In this way, with the aid of improvised models and diagrams, an ideal median section has been reached, the proof of whose approximate accuracy depends on the fact that the various regions in any given oblique section fall into their right position in regard to it.

The accompanying diagram (text-fig. 1) represents the true median section of the seed, and upon it have been plotted the approximate planes of all the more important sections that have passed through our hands, including those referred to in the present memoir. The diagram is in no sense a restoration, the displaced internal tissues are represented occupying the position in which they are usually



TEXT-FIG. 1.—Diagrammatic Median Longitudinal Section of the Seed *Lagenostoma Lomaxi*, upon which are plotted the approximate positions of the planes of section of most of the important sections figured or cited in this memoir. The reference letters and numbers given with each section on the figure are the designations under which the preparations are cited in the text and in the explanation to the plates.

M., M., Median plane; *i.s.*, intermediate sack. W. 1930 should be somewhat nearer the median plane. The small seed in W. 1931A (phot. 1) is not plotted; the section is almost median.

W = WILLIAMSON Collection. M = Manchester Museum Collection.

K = KIDSTON Collection.

LB = University of Lille, Botanical Department Collection.

S = SCOTT Collection.

R = University College, London, Botanical Department Collection.

found in the fossils. It exhibits many of the salient features of the seed, which conforms to the Cycadean type in its general relations. The height somewhat exceeds the diameter, and its figure is that of a prolate spheroid. The full-sized specimens were about $5\frac{1}{2}$ millims. high, and had a diameter of $4\frac{1}{4}$ millims. at the equator. The central body of the seed, the nucellus, is free from the integument in the apical region only for a distance equal to about one-fifth the height of the seed. It consists of a conical or slightly pyramidal pollen-chamber resting on a broad convex plinth, which overlies the chamber of the megasporangium. Around the free part of the nucellus is a massive and rather complicated integument (here termed the canopy) which barely reaches up to the tip of the pollen-chamber, the latter actually protruding beyond the micropyle.

Below the level of separation, integument and nucellus become confluent as in *Cycas*. The wall of the seed throughout is a simple shell consisting of a few layers of elongated fibrous elements limited externally by a well-marked palisade layer, the cells of which bear short peg-like processes. The interior tissue has separated from the wall of the convex sides of the seed in nearly all cases, and hangs suspended like a sack between the pollen-chamber and chalaza. The long gaps shown to the right and left of the intermediate sack in many longitudinal sections (text-fig. 1; and Plate 4, phot. 5; Plate 5, phot. 9) correspond to the peripheral space that has arisen during the decay of the seed. Within the suspended sack the much-contracted megasporangium is usually visible, containing traces of prothallial tissue (phot. 5 and fig. 20).

The vascular system of the seed is derived from a single supply bundle, which shortly after its entry at the base of the seed branches, as a rule, into nine radiating strands. In the majority of specimens these strands run in a plane immediately exterior to the intermediate sack of the seed (text-fig. 1, and Plate 7, fig. 2), though their original position was much closer to the surface. At the apex they enter the several loculi of the canopy and end close to the micropyle.

Around the micropyle the surface of the seed shows nine radially running ridges which die out almost at once. Though standing out in low relief, these ridges form very conspicuous features in oblique sections through the apex when their apparent height becomes much exaggerated, as in the specimen U. C. L., R. 9, c (Plate 5, phot. 10). These ridges are the only external mark of one of the peculiar features of the seed, the radial partitioning of the canopy into nine symmetrically disposed and connivent loculi. Just as the stigmatic bands overlie the placentas of a poppy-capsule, so here are the ridges superposed to the septa of the canopy.

The general relations of the seed, including all the features touched on above, find admirable illustration in the series of three transverse sections from one seed (W. 1915, M.; 1915, O.; S. 236) represented in Plate 7, figs. 1, 2, and 3. This series has a further interest in that the seed, although of full size, was still enclosed in the remains of the cupule. The approximate positions of the three sections are indicated in the diagram (text-fig. 1).

The lowest section (fig. 3) is across the chalazal region just below the plane in which the main vascular bundle breaks into its nine radiating strands. The eccentric position of the fibrous cushion which surrounds the vascular bundle arises from the fact that the section is not truly at right angles to the axis of the seed, an explanation holding good in the other two members of the series as well. The section across the canopy (fig. 1) shows the nine loculi—the radial septa becoming incomplete on that side of the section which dips to a slightly lower level. Within the canopy, with cusps corresponding to its folds, lies the wall of the pollen-chamber, and inside this, like a little circular island, is the transversely cut central cone.

The outside wall of both these sections is very thick in comparison with its true diameter (as shown by the middle section, fig. 2), owing to the nearly tangential plane in which the wall has been cut. In both sections, but particularly in that across the canopy (fig. 1), many series of palisade cells are cut through before the section has done with this layer. And we note the further point that the palisade cells stand in radial files, a result of the meridian-like lines in which the palisade cells are doubtless distributed over the surface. This conclusion finds corroboration from a study of the chalazal section (fig. 3, *pal.*).

The middle section of the series (fig. 2) comes from the broadest part of the seed. It shows the intermediate sack and crumpled megasporangium wall, and, just outside the former, the ring of lenticular tracheal strands. The section is a thoroughly typical one across the middle of a seed. The seed seems to have been generally detached through the agency of a layer of separation formed right across the seed-base at its junction with the pedicel (Plate 10, fig. 26), and all sections appropriately directed in the chalazal region traverse the circular scar below which the abscission-layer was developed. Only a single specimen of a full-sized seed still attached to its stalk has come under our observation (S. 558, fig. 33), though the seed of which the three transverse sections are figured (figs. 1, 2, and 3) may very likely be another instance, as the remains of the cupule are still in position. Unfortunately a study of a section from the same block cut below the seed has been without decisive result (see p. 221, footnote).

In passing to the detailed description of the various parts of the full-sized seed, the following order is observed :—

- (a) The nucellus, with sections dealing with the pollen-chamber, the pollen, and the intermediate sack and megasporangium.
- (b) The integument, including its free and confluent portions, the chalaza and the vascular system.

(a) THE NUCELLUS.

The Pollen-Chamber.

The summit of the free portion of the nucellus is modified to form the pollen-chamber. In form it is bottle-shaped, with the neck just protruding from the

micropyle (Plate 4, photos. 1, 2 and 6, Plate 9, fig. 21). At its insertion upon the convex plinth it undergoes a slight constriction (phot. 6 and fig. 19). The upper third of the sloping surface is bevelled in correspondence with the convexities of the canopy, suggesting that the angles of the former engaged with the grooves of the latter, like a nut in a spanner. This bevelling is shown in all transverse and oblique sections of this part of the pollen-chamber (figs. 20, 22 and 23).

Towards the base of the chamber the bevelling dies out, and the sinus between the pollen-chamber wall and the canopy sensibly broadens in the peripheral direction into a sort of cloister running all round the plinth on which the pollen-chamber stands, and limited externally by the receding slope of the canopy (phot. 6, s., fig. 20, s.).

In the small abortive seeds the sinus is not continued below the base of the pollen-chamber (W. 1931, A. small seed, phot. 2 and fig. 24, s.), as the supporting plinth, no doubt a result of intercalary stretching, had not as yet developed.

The wall of the pollen-chamber is unusually well preserved and was evidently of robust construction. It consists of a single layer of cells, the elements of which have somewhat oblique end-walls (fig. 21, *p.c.w.*). A conspicuous feature of this layer is the relatively great radial thickness of the cells, especially in the lower region of the pollen-chamber, where their tangential walls often project as convex papillæ (figs. 19 and 24). Distally the layer thins out considerably, and in the region of the neck, where it is in close contact with the canopy, it has almost a membranous thinness and is usually much darkened by carbonisation (figs. 19 and 21).

The contour of the chamber varies in different sections according to their plane. The only really longitudinal section, that shown in W. 1931 A. (see phot. 2 and fig. 24), shows it to have been rather truncate in form like a water bottle.

The pear-shaped form seen in U. C. L., R.1 (fig. 19), and the still more tapering outline in U. C. L., R.2 (phot. 8 and fig. 21), both depend on the fact that these sections are oblique (*cf.* text-fig. 1, where the planes of section are plotted). The former cuts the base of the pollen-chamber midway between the centre and the periphery, whilst the latter follows a plane parallel to and close within the sloping wall, which it intersects just above the level of the insertion of the pollen-chamber upon the plinth.

A still more oblique section is shown by the Manchester specimen, K₂. 14257 (fig. 20). This intersects the base at an angle of 45° and then travels out of the pollen-chamber about half-way up the sloping wall. The bevelling of the wall is excellently shown in this specimen. Yet another oblique section of the pollen-chamber is shown in a specimen from the KIDSTON Collection, No. 260 (fig. 22).

The interior of the pollen-chamber is occupied by a cone of delicate tissue which stands erect from the floor. On the flanks this cone is not in continuity with the wall, from which it is separated by a cleft, narrow above but broadening below (*p.c.*, phot. 2 and figs. 19, 21, 24). This space has, no doubt, arisen by the separation of the epidermis from the subjacent tissue. This cleft is the actual pollen-chamber

and it is in its lower third that pollen-grains occur. It is bell-shaped in form and communicates with the exterior at the apex by a circular slit (*o*, figs. 19 and 21).

The tissue composing the central cone is a homogeneous, thin-walled parenchyma, the cells of which are arranged in longitudinal series (figs. 19 and 24, *cc.*). At the base of the chamber the peripheral layers of the cone are continuous with the wall, but elsewhere, both on the flanks and at the base, the tissues of the central cone end abruptly (figs. 19 and 21). Indications of a continuity with the nucellar tissues that survive in the intermediate sack of the seed are not wanting, but of course in full-sized seeds the megasporangium had advanced right into the plinth, so that by its subsequent contraction on the death of the seed comparatively little tissue can have been destroyed (phot. 2).

The cone as a whole, no doubt, represents the apex of the nucellus from which the epidermis has become separated to form the cleft-like pollen-chamber.

The Pollen.

Only four sections of full-sized seeds traversing the lower part of the pollen-chamber have come under observation. Of these the one from Stalybridge (U. C. L., R. 2) contains traces of about six pollen-grains (Plate 5, phot. 8 and Plate 9, fig. 21, *p.g.*, *p.g.*), whilst in a preparation from another seed (U. C. L., R. 1, fig. 19) two are present. In the Manchester section (K₂. 14257) there is a single pollen-grain (fig. 20, *p.g.*), whilst in W. 1930 there is no trace of pollen, although an object is present which, though suggesting a pollen-grain at first sight, is doubtless of fungal origin (phot. 6, to the right of the pollen-chamber, low down).*

The pollen-grains are oval in form and have average dimensions of $70 \times 55\mu$. Indications of an internal cellular reticulum are sometimes shown (fig. 21, *p.g.*), but the state of preservation of the pollen in this species, so far as it has come under our observation, hardly justifies a detailed description. It is much inferior to *Lagenostoma ovoides* in this respect.

No pollen is present in any of the small-sized seeds.

The Intermediate Sack and Megaspore.

The sack-like envelope which stretches from the edge of the plinth below the pollen-chamber to the well-preserved chalazal plate, consists of the collapsed layers that have separated from the shell previous to fossilisation (phot. 7 and 9, *i.s.*).

The separation has usually occurred in the hypoderm of the shell some three or four layers down from the palisade layer, and probably corresponds to the plane in which the softer internal tissues abutted on the harder layer of the integument.

* We have found in other specimens many bodies probably referable to Fungi, both in the palisade layer of the testa and elsewhere.

In the displaced tissues, which morphologically, no doubt, include portions of both integument and nucellus, the most conspicuous feature is the ring of vascular bundles held together tangentially in a thin brown layer of collapsed and discoloured cells (see the specimen W. 1915, O., fig. 2, *i.s.*). This layer has an irregular stratified structure and sometimes shows a tendency to split into two concentric shells (as in U. C. L., R. 6 *b*, fig. 31, *b.r.* and *i.r.*), of which the outer contains the vascular strands, whilst the inner forms the actual pocket containing the megasporangium.

Occasionally an additional detached ring is found outside the bundle-ring (as in U. C. L., R. 9 *b*), but on the whole the mode of splitting of the peripheral tissues is remarkably uniform, giving either a simple intermediate sack (as in fig. 2), or a special bundle-ring with a partly separated inner sack, as in fig. 31).

The original position of these layers is rarely preserved, but in the transverse section across the middle of a seed, U. C. L., R. 7, *b.* (represented in fig. 29), the bundles (*v.b.*) are evidently still *in situ*, though indications of a tendency to split are manifest both within and without the bundle-ring.

The intermediate sack merges below into the well-preserved tissues of the nucellar base (W. 1930, phot. 5 and 7; U. C. L., R. 3, *a*, phot. 9), whilst above it is attached to the trough of the sinus. An inner layer of tissue passes beneath the plinth, and was no doubt continuous with the tissue of the central cone of the pollen-chamber (W. 1931, A. phot. 2). The outer shell, containing the tracheal strands, works round the angle of the sinus and enters the canopy, where it either rests against the inner fluted wall (W. 1930, phot. 6), or more frequently passes upward lying freely in the loculus (U. C. L., R. 3, *a*, phot. 9). These soft internal tissues of the seed are usually much collapsed and distorted in full-sized seeds.

The single megasporangium has contracted away from the interior sack in almost all cases, its thick structureless membrane being thrown into numerous plaitings and corrugations (*e.g.*, W. 1930, M.; Manchester, K₂. 14257; U. C. L., R. 3, *a*, *cf.* phot. 5, fig. 20, *m.g.*, and phot. 9). Its figure is very irregular and in a majority of cases it has retreated into the broader upper region of the central cavity (shown in W. 1930, phot. 5). It often contains traces of prothallial tissue (as in U. C. L., R. 3, *a*, phot. 9), but no indications of archegonia or of an embryo have been recognised.

(b.) THE INTEGUMENT.

Having dealt with the nucellar region of the seed we pass on to the description of its integument and peripheral regions generally. The free part of the integument, the canopy, may be taken first, whilst in succeeding paragraphs the palisade layer, the chalaza, and the vascular system are in turn described.

The Canopy.

This name may be conveniently applied to the whole of the complicated free portion of the integument which forms the hollow, fluted dome around the plinth and pollen-chamber. Its essential peculiarity depends on the fact that it is not a mere sclerotic wall but a series of tangentially joined structures of considerable radial extent and differentiation. The outer surface of the canopy entirely resembles that of the rest of the seed, and there is no external mark indicating the actual zone at which the integument becomes free. Its lining layer, however, is fluted and closely invests the upper portion of the pollen-chamber. It springs from the margin of the plinth, which is slightly cusped, so that even at its actual insertion incipient furrows are already present on this lining layer. That the plinth has an angled contour may be inferred from many longitudinal sections, *e.g.*, U. C. L., R. 1.; W. 1930 (*cf.* fig. 19 and phot. 6), in which its halves are asymmetrical and unequal. That its convex surface bore low undulations is seen in the section U. C. L., R. 3, *a* (phot. 9), where the two obtuse upwardly directed angles of the plinth correspond with the folds in the canopy above.

Before elucidating the structure of the canopy by a consideration of the various sections, it may be explained that the sinus between pollen-chamber and canopy is a conspicuous feature in most sections from this part of the seed, and that in full-sized specimens it formed a roomy cloister below and around the base of the pollen-chamber.

To consider first the transverse sections of the canopy. The lowest of these, cut as nearly as possible horizontally at the level of the base of the pollen-chamber (*cf.* text-fig. 1), is shown in the specimen U. C. L., R. 6, *c*. The section is limited externally by the palisade layer (fig. 30, *pal.*) and underlying hypoderm. Following a space of .5 millim. (fig. 30, *o.s.*), comes a second concentric shell (*b.r.*), and then a third (*i.t.*). The second and third shells are angled, and the outer of the two contains the vascular bundles midway between its angles. The latter is the upper continuation of the ordinary bundle-ring so well shown in the transverse section W. 1915, O. (fig. 2, *i.s.*). The inmost shell is the indurated inside wall of the integument already showing the commencement of the grooving which becomes so conspicuous higher up. The pollen-chamber is not represented as the section is incomplete.

The next section is cut half-way up the pollen-chamber and is from one of the small abortive seeds (U. C. L., R. 11). Externally it is limited by the immature palisade layer upon which abut several layers of hypoderm (fig. 23). From this hypodermal zone spring three arcs, each consisting of a double row of cells. The filling tissue of these arcs has not been preserved and their actual insertions upon the hypoderm are ill-defined for the same reason. Nearer the centre of the figure is the angled wall of the pollen-chamber (*p.c.w.*), evidently displaced.

The deeply grooved layer which the series of arcs collectively form, no doubt corresponds with the inmost shell of the specimen U. C. L., R. 6 *a* (fig. 30, *i.t.*) with its cusps, of course at a higher level (fig. 23, *i.t.*). Although the preservation leaves something to be desired, there is little doubt that the lining layer (*i.t.*), maintains its individuality as it rounds the successive grooves. The points of this layer still show traces of continuity with the peripheral tissue lying below the palisade cells, though in full-sized seeds, in which the softer tissues are rarely preserved, the continuity would be broken and the grooves would lie quite free from the peripheral layer.

The highest of the horizontal sections through the canopy that we have examined is the upper member of the series of three (W. 1915, M., Plate 7, fig. 1). The full number of nine loculi is represented in the canopy. The centre of the section is occupied by the slightly angled pollen-chamber (*p.c.*), and this is surrounded by the fluted, inner wall of the integument (*i.t.*). Of the septa which lie between the loculi, five reach the outer wall, whilst the remaining four fall short. The loculi alternating with these imperfect septa have larger cavities than have those which are completely septate. The explanation is, of course, that the section is slightly tilted so that the chambers on one side are cut at a slightly lower level than on the other (*cf.* plotting of W. 1215, M. in text-fig. 1, p. 197). Those with imperfect septa are cut relatively low down—at a level corresponding to R. 11 (fig. 23)—the others at a higher level where septation is complete, *i.e.*, at which the indurated lining of the furrows and peripheral wall are continuous.

The configuration of the lining of the canopy is somewhat as follows: At its insertion upon the edge of the plinth the organ shows the beginnings of nine radial grooves which deepen as the micropyle is approached. Alternating with these grooves are an equal number of projecting cushions, the convexities of which are directed towards the axis of the seed. This folded organ, resembling an umbrella being opened against a gust of wind, is the internal boundary of the free integument, and by the junction of its upper deeply folded part with the outside wall gives rise to the characteristic "chambers" of this part of the seed. But even after the chambers are complete the double nature of the septa can still be detected. This is shown in W. 1915, M. (Plate 7, fig. 1), also in the oblique Manchester K₂. 14257 (Plate 9, fig. 20), and in the still more oblique KIDSTON 424 (fig. 25). In U. C. L., R. 9, *c* (Plate 5, phot. 10), where the septa are perfectly double, the appearance depends on the fact that they are cut almost longitudinally and not through the narrowest parts of the grooves (for the position of this section *cf.* text-fig. 1, U. C. L., R. 9, *c*).

The relation of the canopy to the sinus between it and the pollen-chamber is well illustrated by a reference to phot. 9, a longitudinal and slightly oblique section through the canopy. The plane of section cuts the plinth midway between its margin and the base of the pollen-chamber. It cuts the chamber of the canopy about its axis almost at right angles, and of course the gaping portions of the two grooves, being cut at right angles, are seen at a minimum. The walls of the left-hand

furrow fail to reach the outside wall, demonstrating how short is the distance from the apex to which the distal ends of the complete septa extend. Though the lower part of the canopy hangs well above the plinth, leaving a roomy cloister, higher up this sinus becomes narrower and chink-like. Indeed the convexities of the canopy probably engaged with the bevelled facets of the upper part of the pollen-chamber wall. This is shown by the transverse section across the canopy in W. 1915, M. (fig. 1), and also by the oblique Manchester section K₂. 14257 (fig. 20), which traverses the base and side of the pollen-chamber, and further by the even more oblique KIDSTON 260, which cuts the upper part of the pollen-chamber at a very steep angle (fig. 22). The detached island of tissue (*i.t.*), in this figure, below the tangentially cut pollen-chamber, is a portion of the sagging wall of the loculus of the canopy which lies in the plane of the section (*cf.* text-fig. 1, K. 260).

The grooving of the interior of the canopy is represented on the outside wall of the seed by the little ridges which radiate from the micropyle, running in the same radial planes as the septa. These ridges are seen in every section that cuts the top of the seed, and in the case of very oblique sections their height is much exaggerated. The true height of the ridges is given by the Manchester section K₂. 14257 (fig. 20, *r*), which cuts the surface near the apex at right angles. Here at a distance of '3 millim. from the micropyle the height of the ridge is 170 μ . In the specimen U. C. L., R. 3, *a* (phot. 9), from a section cutting the ovule $\frac{5}{8}$ millim. from the micropyle, the ridge has practically died out, so that the radial extension of these ridges was trifling. It is in the oblique slices from the top of the seed, such as U. C. L., R. 9, *c*; K. 260 and K. 421, represented in phot. 10, fig. 22 and fig. 25 (*r*) respectively, that the ridges are shown to such advantage, sections in which the ridges are cut very obliquely indeed. The planes in which these sections are cut are shown in text-fig. 1. In Manchester K₂. 14257 (fig. 20) the ridges overlie septa which are cut in the same section; in fig. 22 and phot. 10 the ridges shown belong to the part of the canopy not exposed in the section.

The Palisade Layer.

The surface of the testa is invested everywhere, from the micropyle to the place of insertion of the seed on its pedicel, by a well-marked layer of closely fitting prismatic cells set at right angles to the surface and having a height of 150 μ and diameter of 60–80 μ (well shown in U. C. L., R. 3, *a*, phot. 11). As the separating zone at the seed-base is approached, the layer gradually dies out (*cf.* U. C. L., R. 4, fig. 26, and S. 558, fig. 33). The appearance of the palisade layer, when viewed in superficial tangential sections of the seed, shows that the palisade cells were arranged in longitudinal series, running from pole to pole like circles of longitude (W. 1915, M., fig. 1, *pal.*).

The manner of preservation of the cells varies from seed to seed. In a majority

of cases the walls are relatively thin and carbonised, the cell-contents being relatively inconspicuous (U. C. L., R. 3, *a*, phot. 11). In others, the cavities are filled with dense brown contents, and the walls have a lighter tint (U. C. L., R. 1 and 2, figs. 19 and 21, *pal.*); finally, the walls may be brown and very thick, a type of preservation which, though very usual in the allied species *L. ovoides*, is extremely rare in *L. Lomaxi*.

In most specimens the palisade cells bear little pegs at the surface, not always inserted centrally, and having a height reaching 20–24 μ and occasionally even 30 μ . Commonly these pegs are black and structureless (as in the Lille specimen 1108, fig. 28 A., and U. C. L., R. 3, *a*, phot. 11, *pe.*), whilst occasionally the body of the peg appears to be enclosed in a little cap of membrane (as in U. C. L., R. 9, *a* and *b*, and KIDSTON, 321, not figured). The ordinary type of peg (phot. 11 and fig. 28 A.), therefore, may be regarded as representing the carbonised and persistent contents of little cells exterior to the palisade layer.

In the small abortive seeds the palisade layer is not differentiated. Such seeds are limited by a layer of small cubical cells which bear peg-like papillæ, apparently not yet separated by transverse walls. It may be supposed that at a later stage of development this layer divided tangentially into two layers, of which the inner elongates to form the prismatic layer, whilst the outer survives in the form of pegs.

In the immediate neighbourhood of the micropyle the cells of the testa project as well-marked papillæ (W. 1931, A., fig. 32). These papillæ are not isolated quite in the same way as the pegs just described, but probably correspond to the distal ends of the mother-cells with which they remain, perhaps, in open connection.

The knob-like preservation of the surface layer, found in the young seed U. C. L., R. 13 (*cf.* p. 213), perhaps owes its origin to the entire contents of the layer of mother-cells being preserved in much the same way as are the pegs on full-sized specimens (*cf.* fig. 34, *pal.*).

There is a further peculiarity of the palisade layer deserving mention, in which the pegs seem to play a passive rôle. The latter are sometimes found raised up on tapering cones (as in the Lille specimen 1108), as though some mucilaginous substance had been emitted from the prismatic cells below, or from the wall upon which the pegs are seated (fig. 28 B.). In extreme cases the black pegs are raised to a considerable height in this way (U. C. L., 8, *b*, phot. 12, *pe.*). This phenomenon, as we find it in these seeds, was a local effect, and resulted in a blister-like raising of the organic *débris* by which the seed was closely invested (phot. 12, *mu.*, in which the mucilage cones are clearly shown). But although, perhaps, having their origin in some local lesion, it seems not improbable that the blisters observed by us are merely a sporadic and premature manifestation of a phenomenon which normally became general only at a latter stage in the history of the seed. This mechanism suggests comparison with the mucilaginous testas of many recent Angiospermic seeds.

The Chalaza.

This region of the seed is characterised by the relatively large amount of sclerotic tissue that is present at the seed-base. The thin shell of the seed expands abruptly to form a funnel-shaped cushion or cup, in the cavity of which the base of the nucellus rests (well shown in the median section W. 1930, phot. 7).

The chalaza is sharply defined below by the layer of separation which completes the surface of the adult seed where it was attached to its stalk (phot. 7, *a.l.*). The only full-sized specimen still remaining on its pedicel (S. 558, phot. 15 and fig. 33) shows the layer of separation (*a.l.*) cutting across the tissues in such a way as to leave a low projecting cushion on the seed when it became detached. And all the other seeds cut in an appropriate plane agree in showing a convex cicatrix. When the section cuts the scar in the median plane (as in phot. 7) the cushion is shown to be conical, but most sections across the cushion miss the tapering apex. The surface of the papilla is covered with about two layers of small iso-diametric cells (U. C. L., R. 4, fig. 26), in connection with which the severance took place.

Just within the papilla and occupying its whole width is the funnel-shaped sclerotic cushion. The elements which compose it are long and fibrous; they have fairly thick walls, and the contents are more or less blackened. At first these fibres run parallel to the long axis of the seed, but soon they diverge like a brush and the peripherally placed fibres take a superficial course below the palisade of the testa and form the hypoderm of the shell throughout the seed (U. C. L., R. 4, fig. 26, *hy.*). The interior fibres diverge less sharply and form a thick and closely knit sheath symmetrically disposed around the axial supply-bundle on its entry from the pedicel (*cf.* the median sections W. 1931 A. and W. 1930, photos. 3 and 7, *ch.c.*). The sclerotic character of these cells ceases abruptly at a distance of $\frac{1}{2}$ – $\frac{2}{3}$ millim. from the scar, and their further continuation is at best represented for a short distance by a more or less collapsed reticulum of loose strands which corresponds to the insertion of the softer peripheral tissues of the seed-base.

The hollow in the sclerotic cushion has the form of a champagne glass (phot. 7, *v.b.*), and as the bowl expands the entering bundle separates into the peripheral vascular strands, which run in the plane of the glass.

Such sections as are not median, but cut the chalazal papilla between its periphery and the centre and then run up obliquely in a direction *away from* the axis of the seed (*cf.* text-fig. 1, S. 558; U. C. L., R. 4), pass more or less tangentially along the sclerotic cushion, so that this structure is shown with a convex upper boundary (see the specimens S. 558, and U. C. L., R. 4, figs. 33 and 26, *ch.c.*). Again, in other sections which start like the last, but take an oblique direction *towards* the axis of the seed (text-fig. 1, Lille 1110), the relation of the parts must vary according to the plane followed. The section of the Lille specimen, 1110 (fig. 27), intersects the bundle at its place of branching and almost coincides with the limiting slope of

the bundle-socket on the distal side (*cf.* text-fig. 1). Thus, two of the branch-bundles are exposed in longitudinal section for some distance (fig. 27, *b* and *c*), and the section eventually traverses the corner of the intermediate sack or megasporangium, of course cutting others of the vascular strands *d*, *e*, *f* higher up as they pass towards the apex. The specimen U. C. L., R. 7, *a* (not figured) is a section following an almost identical plane (*cf.* text-fig. 1, p. 197).

Transverse sections near the base of the seed, such, for instance, as the lowest of the series of three, S. 236 (fig. 3) and U. C. L., R. 8, *a* (phot. 13), show the chalazal cushion as an annular zone of transversely cut fibres with the supply bundle (*v.b.*) occupying the centre. Around the cushion is a gap bridged at places by the shreds of looser tissue, whilst peripherally the seed is closed in by the hypoderm and palisade layer. The multi-seriate appearance of the last-named is an obvious consequence of the almost tangential plane in which the testa is cut.

The eccentricity of the several zones in both these sections depends, of course, on the fact that the plane of section is not truly transverse (*cf.* text-fig. 1). In this part of the seed even very slight changes in the angle of cutting lead to marked alterations in the distribution of the various zones.

Overlying the sclerotic cushion is a somewhat concave plate (W. 1930, and U. C. L., R. 3, *a*, fig. 5 and phot. 9, *nu.*) forming the bed upon which the base of the intermediate sack rests. It is loosely compacted of thick-walled oval cells, whose longer axes usually run in the radial direction. Thus, in the specimens U. C. L., R. 4 and R. 3, *a* (fig. 26 and phot. 9), these elements are cut nearly transversely in the middle parts of the section, in the Lille specimen 1110 (fig. 27, *nu.*) almost longitudinally.

Peripherally the edges of the bed or plate bend up and become continuous with the sides of the intermediate sack.

The Vascular System of the Seed.

The bundles that traverse the seed form a conspicuous feature in almost every preparation, alike of older and younger specimens.

The vascular supply is derived from the chalazal bundle that enters at the seed-base by its subdivision into a whorl of nine bundles, which range themselves symmetrically around the intermediate sack and pass distally into the loculi of the canopy.

The chalazal bundle follows the axis of the seed in its passage through the chalazal cushion. At a distance of $\frac{1}{2}$ – $\frac{3}{4}$ millim. from the scar at the seed-base it expands into a funnel (Plate 7, fig. 5) and breaks up into the nine peripheral bundles which at once bend sharply outwards and shape their course so as to round the base of the intermediate sack of the seed. The connection between the chalazal and peripheral bundles for each category of seed is well shown in the three median sections that are

figured: In the young seed or ovule, U. C. L., R. 13 (fig. 33, *a*); in the small abortive seed, W. 1931, A. (Plate 4, phot. 3); and in the full-sized specimen, W. 1930 (phot. 7 and fig. 5). The place of branching of the chalazal bundle is also cut in several of the oblique sections through this part of the seed, a type of section well illustrated by the Lille specimen 1110 (fig. 27). This figure shows three divergent bundles, *a*, *b* and *c*, of which *b* and *c* are cut nearly in longitudinal section. Other similar sections, such, for instance, as U. C. L., R. 7, *a*, are in essential agreement.

Of the chalazal bundle below its point of branching two sections are figured. The lowest member of the series of three sections of one seed (S. 236), illustrated generally in fig. 3, cuts this bundle transversely. An enlarged view of the same bundle is given in fig. 4, and a longitudinal section from W. 1931, A., in fig. 5. Another specimen, also cut transversely, is clearly indicated in U. C. L., R. 8, *a*, (phot. 13, *v.b.*).

The nine branch-bundles after rounding the base of the nucellus make their way upwards in most specimens in the collapsed layers of soft tissue which collectively form the intermediate sack of the seed. The oblique Lille section (1110, fig. 27) shows three of these bundles (*d*, *e*, *f*) shortly after turning the corner of the megasporangium, whilst transverse sections across the middle of the seed (of which W. 1915, M., fig. 2 is a perfectly typical example) are characterised by a circle of nine bundles, withdrawn some distance from the periphery of the seed, and connected together by the intermediate sack. In longitudinal sections the number of bundles cut of course depends upon the obliquity of the section (*cf.* phot. 5, phot. 9, and fig. 20).

The true position of these bundles in the body of the seed is demonstrated by the section U. C. L., R. 7, *b* (fig. 29), where they are found *in situ*. The single bundle represented in this figure (*v.b.*) is still in continuity with the hypoderm (*hy.*), and is separated from the superficial palisade layer by about five layers of cells.

As the bundles approach the apex they pass outside the periphery of the plinth and enter the canopy, one to each loculus (figs. 1, 23, and 30). That the bundles cling very closely to the outside angle of the sinus (see photos. 6 and 9 and fig. 20) seems to be due to the fact that in this region, as in the body of the seed, they have suffered a centripetal displacement. No section, however, has passed through our hands in which the bundles at this height are seen lying *in situ*, though in the specimen U. C. L., R. 6, *c* (fig. 30, *v.b.*) their position is probably not far from that which they occupied in the living seed. That a single bundle normally entered each of the nine loculi of the canopy is shown by almost every section through this part of the seed (figs. 1, 20, 23, 25), though the bundles are not always preserved, especially in the distal parts of the loculi.

The form of the chalazal bundle in transverse section is roughly circular with dimensions for the xylem strand of $84 \times 70\mu$; the peripheral bundles, on the other hand, have an elliptical section (W. 1915, O., phot. 14), with average dimensions at

the mid-height of the seed ranging from $160-176\mu \times 60-70\mu$. The major axes of the bundles lie in the tangential plane.

In their passage to the apex of the seed the strands taper to some extent, but they retain the elliptical outline throughout.

In one instance a bundle was found to fork in passing from the chalaza to the canopy. The section of the central seed, of the row of three full-sized specimens in the preparation W. 1931, passes through the basal half and shows a ring of nine bundles. A second section higher up this same seed occurs in the KIDSTON preparation No. 260. In this section there is a ring of ten bundles. This is the only departure we have met with in *Lagenostoma Lomaxi* from the constant number of nine peripheral bundles. That this is a case of a bundle forking on its way up the seed rather than a fusion of two bundles depends, of course, on the correct determination of the relation of the two sections. In the absence of any trace of the chalazal tissues or of the canopy or pollen-chamber in either of the sections, the recognition of W. 1931 as the lower section is based on the relative diameter of the intermediate sack in the two sections in question. In W. 1931 the sack is 2 millims., and in KIDSTON 260 it is 3 millims. in diameter. As the intermediate sack is well known to expand like a funnel in its passage up the seed (e.g., specimen 1930, phot. 5), there is no doubt the smaller ring belongs to the lower section.*

The peripheral position of the bundles, as determined by the specimen U. C. L., R. 7, b (fig. 29), and the fact that they run into the free part of the integument or canopy, seems to stamp the bundles as definitely appertaining to the integument of the seed.

Turning now to the *structure* of the seed-bundles, it is mainly the xylem strands that are preserved. In the transversely cut chalazal bundle in the specimen, S. 236 (fig. 4), the xylem is shown with its smallest elements at the centre. In the slightly disorganised zone of soft tissue which accompanied the xylem strand it is not possible to differentiate the phloëm. The very similar section U. C. L., R. 8, a (phot. 13) shows the position of this zone, but it is much more disorganised.

The chalazal bundle is cut in longitudinal section in the specimen W. 1930 (phot. 7, v.b.). The enlarged drawing (fig. 5, p.x.) shows the small protoxylem elements to be centrally placed, thus confirming the indications given in the transverse section (S. 236, fig. 4). The chalazal strand is consequently mesarch.

In the branch-bundles, as seen in transverse section, the smallest xylem elements occur along the face directed towards the centre of the seed (W. 1915, O., phot. 14), or they may lie a little deeper in the strands (as in U. C. L., R. 8, b). The radial section of a bundle from a full-sized seed in W. 1931, A. (fig. 6) shows the sequence of the various elements. The protoxylem element (p.x.) lies close to the internal side of the strand, from which it is separated by another spiral element of slightly larger calibre. The other tracheides are spiral and scalariform, and in one case pitted. Similar indications are given by one of the bundles in KIDSTON 321. It

* The positions of the two sections are shown on the diagram, p. 197, at K 260-2 and W 1931-2.

thus appears that these peripheral strands are either endarch or very nearly so, the amount of centripetal xylem being, at the best, trifling. Some of the narrow elements shown accompanying the xylem in fig. 6 may be phloëm, but we are unable to speak confidently as to this part of the bundle as the indications are so slight.

In nearly all cases in which the structure of the peripheral bundles is shown in longitudinal section, and especially in those cases in which spiral elements have been recognised, it is in the lower part of their course. This is hardly to be explained as being due to the greater dimensions of the bundle below than above. It may perhaps be correlated with the fact that the upper part of the seed undergoes a relatively late extension. The only ground for this suggestion is the fact that the plinth is wanting in the small abortive seeds (phot. 2), so that in passing from the small to the full grown dimensions there must have been considerable intercalation in that particular zone of the seed.

The Abortive Seeds.

Besides the full-sized specimens, having approximate dimensions $5\frac{1}{2} \times 4\frac{1}{4}$ millims., there are the small, though in many respects mature-looking, seeds to which reference has already been made. Their dimensions are $2\frac{1}{2} \times 2$ millims.

Two of these smaller seeds have been found cut in longitudinal section, whilst in three other specimens parts of the canopy and pollen-chamber are shown.

The specimens are—

W. 1931, A., the smaller seed on this slide.

It is cut quite longitudinally and is still enveloped in its cupule (see phot. 1).

W. 1931, a small seed occurs at the edge of the section.

It is cut less medially than the last and like it is completely enveloped in its cupule (see phot. 4).

W. 1915 R., a transverse section across the canopy and pollen-chamber, with parts displaced.

U. C. L., R. 11, a section resembling the last, but nearer the apex.

U. C. L., R. 12, a median longitudinal section of pollen-chamber and canopy.

In their *form* these seeds differ slightly from the full-sized type.

If the small seed W. 1931, A. (phot. 1) be compared with the full-sized specimen W. 1930 (phot. 5), both being almost median sections, the former is found to be relatively stouter than the latter, *i.e.*, the ratio of the transverse to the longitudinal diameter of the little seed is in excess of that of the full-sized seed. Further, the small seeds are somewhat more barrel-shaped than the large ones, their sides being relatively less convex.

The slight broadening towards the base shown by the specimen W. 1931, A. (see phot. 1) is probably the result of an injury which its chalaza sustained prior to

fossilisation, the chalazal cushion having been displaced some little distance into the interior of the seed.

As regards their *structure*, both the pollen-chamber and chalazal cushion of the small seeds are of full size, but the convex plinth which supports the former in the full-sized seed is here undeveloped. The sinus around the pollen-chamber is not continued beyond the base of the pollen-chamber. The plinth doubtless arose later by intercalary stretching in the zone below the pollen-chamber. The elongation referable to this cause alone corresponds to 20 per cent. of the total stretching that the seed must have undergone in passing from the arrested to the full dimensions.

The parenchyma flanking the central space is well preserved, particularly in the section of a small seed in W. 1931 (phot. 4), which, being cut somewhat tangentially lies in the plane of the intermediate sack. The vascular strands are completely differentiated, though they do not afford any special indications lacking in the larger seeds. The entering bundle in the small specimen W. 1931, A., as it expands at the base of the nucellus (phot. 3) is the counterpart of the strand as shown by the full-sized seed W. 1930 (phot. 1, *v.b.*).

The outer wall of the integument in small seeds presents certain peculiarities. The shell as a whole is thinner than in normal seeds (70μ as against 190μ), but its tissues do not appear to have been softer or less rigid than those of the mature specimens. The little seed in W. 1931, A. (phot. 1) has preserved its contour quite as fully as has the large seed in W. 1930 (phot. 5). The basal region perhaps may have been somewhat deficient in strength, as evidenced by the collapsed state of the chalaza in the former specimen. The tall palisade layer of the normal seed is represented here by a much smaller and nearly cubical cell-layer about one quarter the height (*cf.* phot. 11, and fig. 23, *pal.*). In both cases pegs are present on the surface, but whilst in the old seed the peg may reach a length of 25μ , in the abortive specimens they do not exceed $10-12\mu$ in height. Further, in the small seed the peg does not appear to be separated as a distinct cell, though in the normal condition it seems probable that such a separation occurred.

The most interesting features shown by these small seeds are: (1) The matured appearance of the tissues, especially of the shell, pollen-chamber and chalazal cushion; (2) the full size of the pollen-chamber, which, though it projects to the exterior, is without pollen-grains; (3) the absence of the plinth.

These specimens fell through the agency of the abscission-layer, the base of the seed being sharply isolated in both the complete examples (phot. 3 and 4, *a.l.*). The cupule, still closely investing the seed, fell with it, forcibly wrested from the pedicel after the separation of the seed.

The Small Seed or Ovule.

In addition to the abortive seeds, described in the last paragraph, another small specimen U. C. L., R. 13, has been examined which shows rather peculiar features.

The seed itself, which has a length of about 2 millims., is much altered and not easy of interpretation. The pollen-chamber, chalaza, and cupule alone are well-preserved, whilst the main body of the seed is much crumpled and the testa exhibits extreme decay. In all probability the specimen is a young or ovular stage with immature tissues. The section is longitudinal and median, and shows the seed and cupule both attached to the pedicel. The testa of the seed is represented by an extraordinary, irregular mass of dark strands, covered on the surface with black pegs, recalling those on the normal testa but longer (*cf. fig. 34, pal.*). The black pegs or knobs occur in all sorts of positions—not only towards the exterior. This is to be accounted for on the supposition that the testa is completely crumpled up and thrown into folds which the section cuts across at various angles. The knobs probably represent the entire contents of a disorganised mother-cell layer from which palisade layer and pegs normally develop.

The interior of the seed is occupied by three curious black-walled pipes (*fig. 34, i.s., i.s.*) which run longitudinally—one above reaching up to the base of the central cone of the pollen-chamber, and two below, not far from the chalaza. These probably are the remains of the much-shrivelled nucellus and megasporangium. Closely accompanying these structures, on either side and also between them, are the vascular bundles—an appearance due to the extreme shrivelling that the tissues have undergone. Throughout the specimen the vascular bundles are extremely well preserved. At the chalaza the branching of the main bundle is shown (*fig. 34, ch.*), and it can be traced right back into the pedicel where the insertion of one of the cupular bundles may be seen (*at a*). This is the only specimen we have met with showing the origination from the main vascular strand of both the cupular and peripheral seed-bundles. The cupule of this specimen is described below, p. 215.

POLLINATION.

A majority of the sections that traverse the lower part of the pollen-chamber of full-sized seeds afford evidence that pollination has been effected. The supposed ovule (U. C. L., R. 13, *fig. 34*), and the small arrested specimens, on the other hand, contain no pollen.

Nevertheless these young seeds were already provided with pollen-chambers of full size and mature appearance, whilst the orifice, also, projected well beyond the canopy (*phot. 2 and fig. 24, p.c'.*).

These facts are consistent with the view that pollen was received by the seed while it was still fairly small; as soon, perhaps, as the unfolding of the cupule at the apex permitted. Nevertheless we hardly possess sufficient data for arriving at a decision as to the time of pollination. The little seeds seem ready for the pollen, but only full-sized specimens are known to contain pollen in the pollen-chambers. The reason, too, for the abortion of the small-sized seeds remains obscure. In view of

what is known to happen in the case of Cycads, it would be imprudent to conclude that abortion occurred from lack of pollination.

The full-sized pollinated seeds seem to have fallen through the agency of the abscission-layer, and but rarely to have remained involved in the cupule (as in the series represented in figs. 1, 2 and 3). That the specimen S. 558 (photos. 15 and 16) is still attached to its stalk was no doubt the result of accidental circumstances. The process of fertilisation probably took place on the ground. To an elucidation of the further history of the seed there are no data to guide us. It may be conjectured that it was not altogether unlike that of existing Cycads.

As regards the mode of pollination, how the pollen was brought and retained, just this can be said. There was in all probability a drop-mechanism at the tip of the seed by means of which the grains of pollen were retained and sucked or siphoned into the pollen-chamber, much as in recent Gymnosperms. Whether such a drop originated directly from the orifice of the pollen-chamber, or whether perhaps the tips of the loculi of the canopy may have co-operated in this service, must remain a matter for conjecture.* That the pollen was borne to the seed by the wind should not be tacitly assumed in the case of *Lagenostoma*. The protruding pollen-chamber and the presence of glands on the cupule suggest a possibility of the co-operation of insects.† Although the not very numerous available sections of the pollen-chamber of *L. Lomaxi* are inconclusive as to the amount of pollen that was delivered to this seed, the case is otherwise with the closely related *L. ovoides*. Here the evidence afforded by an extensive series of appropriate sections points to the existence of an unusually perfect mechanism for pollen-transfer. The pollen-chamber is, as a rule, abundantly provided with pollen-grains and sometimes it is almost choke-full. Taken in connection with the points already mentioned, the case of *L. ovoides* would seem to indicate a mechanism of pollen-transfer of greater precision than chance dispersal by wind. The question is one deserving further consideration, though we cannot pursue it here.

Summary for Seed.

Lagenostoma Lomaxi is an orthotropous seed of Cycadean organisation. It shows complete radial symmetry. Specimens of full size are about $5\frac{1}{2}$ millims. long and $4\frac{1}{4}$ millims. in diameter.

The central part of the seed is generally contracted away from the testa forming the intermediate sack in which the crumpled megasporangium is contained.

The apex of the nucellus alone is free from the testa from which it protrudes. It

* Cf. 'Annals of Botany,' vol. 17, p. 462.

† Our attention was drawn to this possibility, which we had not considered, by Sir JOSEPH HOOKER in a letter to one of us. The passage containing the suggestion raises a point of the greatest interest and we quote it in full: "What can be the meaning of the capitate glands? They would seem to indicate the contemporaneous insect life which I think has been demonstrated to exist in the Coal Measures. Has any

is modified to form a pollen-chamber by the separation of its epidermis from the central tissue. Pollen-grains are found occurring in the bell-shaped chink thus formed.

The testa is coalescent with the body of the seed for four-fifths of its height. Around the apex of the nucellus it stands free as a complex chambered organ, the canopy. The micropyle does not extend as a pore or passage above the pollen-chamber, as in most other seeds, but encircles the narrow angled tube of the pollen-chamber like a spanner on a nut.

The free part of the integument or canopy is septate towards the apex, whilst lower down, the septa, usually nine in number, give place to deep furrows on the inner face. These furrows gradually flatten out as the plane of insertion of the canopy on the body of the seed is approached.

The outer surface of the testa is covered with a continuous palisade layer, the cells of which bear little peg-like outgrowths. At the summit the surface is thrown into sharp radially running ridges, nine in number, overlying the septa of the canopy.

The chalaza is of solid construction, and is penetrated by a single centrally placed vascular bundle which breaks up into nine peripheral strands. These run just below the surface of the seed and make their way one to each loculus of the canopy.

The seed was detached from its pedicel by a layer of abscission formed across the seed-base.

In addition to the full-sized seeds, smaller specimens occur. These are about $2\frac{1}{2}$ millims. in length and are generally found completely enclosed in the cupule, a husk-like sheath which springs from the pedicel just below the insertion of the seed. These small seeds have a full-sized pollen-chamber but contain no pollen. The testa is mature looking, and these seeds were probably abortive.

One specimen of an ovular stage has been found.

THE CUPULE.

The specimens at present known, in which the seed *Lagenostoma Lomaxi* is seen in connection with its cupule, are six in number. They are as follows :—

WILLIAMSON Collection, 1931	Longitudinal section.
” ” 1931, A	” ”
” ” 1915, M	The series of three transverse sections from the same seed.
” ” 1915, O	
SCOTT Collection, 236	

one accounted for the quantity of pollen-grains in the sac of the ovule of Cycadeæ—so many more than the wind is likely to have brought ?”

The suggestion, in any case a valuable one, gains in weight when it is remembered that the first account of the structure of a Coal-measure seed, in a paper that has become classic, was written by Sir JOSEPH HOOKER (“*Trigonocarpon*,” ‘Phil. Trans.’, vol. 145, 1855), and that his conjecture that the flowers of *Welwitschia* were pollinated by insects has received general acceptance (‘Linn. Soc. Trans.’, vol. 24, 1863).

WILLIAMSON Collection, 1915, P	Longitudinal, crushed.
SCOTT Collection, 558	„ showing pedicel.
U. C. L. Collection, R. 13	„ of young seed or ovule.

The most important sections showing the cupule detached from the seed are the following :—

R. Holloway College Collection, H. 55 . . .	Transverse section.
U. C. L. Collection, R. 14, a	Longitudinal and transverse sections, perhaps all from the same cupule.
„ „ „ R. 15	Longitudinal, showing pedicel.

Isolated fragments of the cupule are frequent, and in some cases, no doubt, belong to the same specimens which, in adjacent sections, are shown attached to the seed.

In the case of the detached cupules, the agreement in structure with those attached to the seed indicates *L. Lomaxi* as the species, but there is a bare possibility that some of these may represent the cupule (otherwise unknown) of *L. ovoides*, as the two species occur together.

From these various specimens a fair idea of the form and structure of the cupule and of its relation to the seed can be gained.

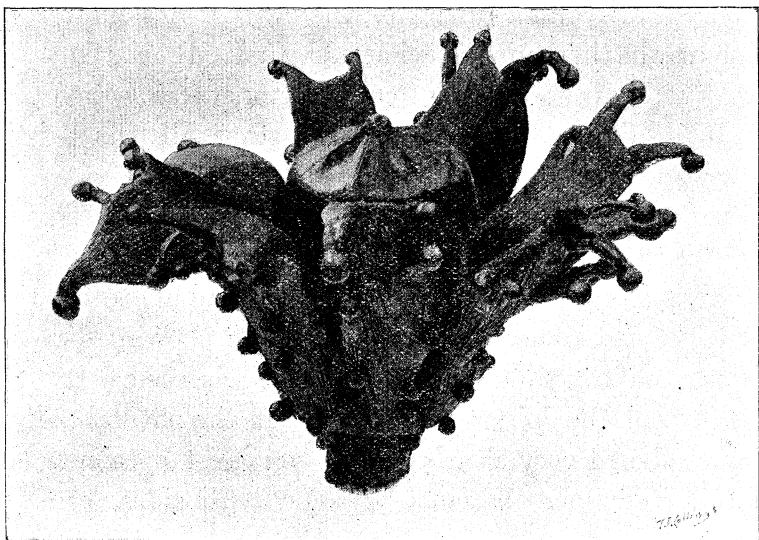
Form of the Cupule.

In some of the specimens showing seed and cupule in connection, the seed was of full size or nearly so* (the transverse series, W. 1915, M., &c., S. 558, and probably W. 1915, P.). In others the seed, though perfectly developed, is small (W. 1931 and 1931, A.), measuring 2·4 millims. and 2·2 millims. in length, as against 5 millims. or more in the mature seed. As pointed out above (pp. 195 and 211) these two specimens appear to represent an arrested condition of the young seed. In another case above described (p. 212) the seed, though scarcely smaller than the arrested specimens, appears to have been in the normal young or ovular condition, and is consequently badly preserved (U. C. L., R. 13). These three young or arrested specimens give the best idea of the general form of the cupule and its relation to the seed (see Plate 4, photos. 1 and 4 and Plate 10, fig. 34). At this stage the cupule far overtopped the seed, and no doubt completely enclosed it. In the youngest specimen (fig. 34) a lobe of the cupule even extends to double the height of the ovule, but here some displacement may have occurred. At maturity the enclosure of the seed was no doubt less complete. The transverse section W. 1915, M. (Plate 7, fig. 1) shows that even in the mature condition the cupule still reached to near the apex, but at this stage it

* Measurements of the seed are given above, p. 198.

was in all probability open at the top, as shown by the fact that most of the seeds found had freed themselves from it altogether.

The seed was borne terminally on a pedicel, as seen in the longitudinal section S. 558 (Plate 5, phot. 15 and Plate 10, fig. 33), the only case in which the connection is shown in a mature specimen ; the seed, though cut tangentially, measures 4·5 millims. in length by 2·8 millims. in maximum width. The pedicel is shown for a length of about 2 millims., but as it is incomplete below, no idea of its real length can be formed. It is about 0·5 millim. in diameter. The cupule springs from the pedicel at its upper end, immediately below the base of the seed, which it closely invests. In cases where the investment is loose this may be due to accident or to the arrested growth of the seed (Plate 4, phot. 1, from W. 1931, A.). The cupule in its lower



TEXT-FIG. 2.—Photograph from a large Wax Model of a Restoration of a small-sized Seed of *Lagenostoma Lomaxi*, enclosed in its Cupule. Model prepared by Mr. H. E. H. SMEDLEY.

part formed to all appearance a continuous envelope, as is shown most clearly in a section kindly lent by Miss BENSON (see Plate 7, fig. 7). This is a transverse section of a cupule, at once identified by the glands as belonging to the *Lagenostoma Lomaxi* type. The diameter is 3 millims. The seed itself is not present, but the central mass of tissue, which is partly preserved, agrees with that shown at the base of the seed in other specimens (e.g., S. 558, U. C. L., R. 15, cf. figs. 9 and 33, also photos. 15, 16). The dimensions also correspond, and there is little doubt that this section is from the lowest part of the cupule, on a level with the base of the seed. Here the cupule is evidently continuous all round, except for accidental fractures. We have no certain evidence to show to what distance upwards the cupule remained undivided. In the lowest of the series of three transverse sections (S. 236, see fig. 3) the cupular tissue is continuous for an extent of about 4 millims., representing about two-fifths of the periphery in this region. The rest of the cupule is much broken,

and one side of it bent back, the reflexed portion extending to the lobed region above (fig. 3). We have no evidence that the cupule divided into two valves, as in M. RENAULT's *Gnetopsis* ;* this is not impossible, but more probably it remained continuous until it broke up into the terminal lobes to be described below.

Returning to Miss BENSON's section, the cupule at this level is very conspicuously ribbed (fig. 7), a character less evident in the other specimen (*cf.* fig. 3). It appears even more deeply furrowed on the inner than the outer surface ; there is no indication of this in other transverse sections, and it must probably be regarded as an effect of contraction and rupture of the tissues. The external ribbing was no doubt to some extent natural. Additional evidence for this is afforded by the longitudinal section S. 558 (Plate 5, phot. 15, and Plate 10, fig. 33), where the cupule appears about twice as thick on the left hand side as on the right. Presumably the section passed through a ridge on one side and a furrow on the other. A similar difference between the two sides is shown in the young specimen U. C. L., R. 13 (fig. 34). The number of ridges, if we may judge from the one complete transverse section (fig. 7), was about ten or twelve. It is difficult to determine whether all the existing protrusions were present during life.

In its upper part the cupule broke up into separate lobes. This is clearly shown in the small seed (W. 1931, A.) represented in longitudinal section in Plate 4, phot. 1. The section as a whole is median, but the part of the cupule to the right is evidently displaced, so as to be cut almost tangentially, thus showing two lobes connected below. Lower down on the same side a third lobe is seen. It is often difficult to make out to what extent the lobes were separate in the natural state. That laciniæ existed is certain, as shown very clearly in the youngest specimen (U. C. L., R. 13, fig. 34), where a narrow lobe, bearing hairs on both sides, can be traced to its termination. It is probable, however, that the depth of the fissures between the segments may have been exaggerated by tearing or decay in the weak parts between the ridges, for the edges of the apparent lobes are by no means always clean and definite. In the transverse series of sections, which should throw most light on the segmentation of the cupule, this part of the specimen is unfortunately too fragmentary to give any certain information on the point. In the middle section (W. 1915, O., fig. 2) the portion of cupule at *c'* appears to have natural limits ; this piece is about 2 millims. long, corresponding to about one-sixth of the periphery, it may represent two lobes not yet separated from each other. In the uppermost section of the series (W. 1915, M., Plate 7, fig. 1) there is still a continuous piece of cupule nearly as long as that in the previous sections, indicating perhaps that even so high up as this the lobes had not yet completely separated ; the fragment in question is thinner at some points than at others, which may be a sign that further segmentation was in progress.

The specimen U. C. L., R. 14 (Plate 6, phot. 17, and Plate 8, fig. 11) shows the cupule

* 'Cours de Bot. Foss.', vol. 4, p. 180, Plate 20, figs. 7-10, 1885.

in approximately tangential section, parallel to the surface. It gives little definite evidence of lobing up to a height of about 3 millims. from the base ; we cannot assume that its ragged edges really represent the outlines of natural segments ; they may well be due to the section passing out somewhat obliquely through the ribbed surface.

From the data available we may conclude that the cupule of *Lagenostoma Lomaxi*, springing as a cup-shaped envelope from the pedicel, remained undivided for half its length or more, and then broke up into a number of lobes or laciniae ; the latter may have become more deeply severed by subsequent splitting, which quite possibly occurred in the normal course of development.

Structure of the Cupule and Pedicel.

The cupule was traversed throughout its length by a number of vascular bundles, which branched off from the single strand of the pedicel.

The specimen which best exhibits the structure of the pedicel is the longitudinal section S. 558, already mentioned (Plate 5, phot. 15, and Plate 10, fig. 33). The section is tangential, as shown by its missing the micropyle and chalazal bundle of the seed ; it approaches the median plane more nearly in its lower than in its upper part. The central bundle of the pedicel can be followed to within '5 millim. of the abscission-layer at the base of the seed ; towards its upper end the bundle is clearly sending off a branch to the right, to enter the cupule ; on the left a vascular bundle can be traced for a long distance through the cupule (phot. 16 and fig. 33), but its connection with the strand of the pedicel is missed.

The connection between the cupular strands and that of the pedicel is better shown in the young specimen, U. C. L., R. 13, which is seen in median section (fig. 34). Here the central strand can be followed all the way to the chalaza of the ovule, where the vascular system of the integument branches off (see above, p. 213). About '8 millim. below this point, a bundle diverges from the main strand at an acute angle, to gradually pass out into the cupule, through which it can be traced for some distance. Thus the relation of the bundle-systems of integument and cupule is clearly shown.

Another section of great value as showing the course of the cupular bundles is that represented in Plate 6, phot. 17, and Plate 8, fig. 11 (U. C. L., R. 14). This is the tangential section of the cupule ; the base is towards the left of the figure. A number of vascular bundles (lettered *a-i* in the figure), are present ; the principal strand (*a*), is about 300μ in diameter ; it is only shown for a short distance and then branches out immediately into the three strands (*b*, *c* and *d*). The remaining bundles (*e-i*), also converge towards the principal strand or group, though their connection with it is missed. Probably all the bundles shown belong to the cupule, except the principal strand *a*, which, from its large size (much exceeding anything met with in the cupule

proper), can only represent the upper end of the central strand of the pedicel. The bundle *c*, which from its position, lying in the direct continuation of *a*, might be taken for the chalazal strand, is more probably one of the cupular bundles, for it differs in no way from the others, and no trace of the chalaza is to be found. The main strand *a* is obliquely cut, and its prolongation into the chalaza probably lay outside the plane of section. This specimen shows clearly how the main strand of the pedicel sent out branches on all sides into the cupule, which they traversed, eventually entering its terminal lobes (*cf.* fig. 34, from U. C. L., R. 13). That the cupular bundles themselves branched is certain, for the strands *g* and *h* (fig. 11), are clearly diverging from a common origin; a branching cupular bundle is also shown in phot. 1 (from W. 1931, A.), towards the right.

Our best evidence as to the number of bundles which entered the cupule is derived from the section (H. 55), lent by Miss BENSON; this, as we have seen, was cut transversely, about at the level of the base of the seed (Plate 7, fig. 7). The cupule here contains nine or perhaps ten recognisable bundles, of which two appear to be double and may represent points of branching. It is very likely that one or two other strands, no longer to be detected in the imperfectly preserved tissues, may have been present.

In the lowest section (S. 236), of the transverse series of three, cut at the level of the chalaza, seven bundles are shown in the very imperfect cupule (fig. 3). One of these strands is double and has evidently just branched. In the middle section of the same series, W. 1915, O., cut about half-way up the seed, seven bundles are seen in portions of the cupule occupying collectively scarcely half of the periphery (fig. 2); one of these strands is double.

It thus appears that the base of the cupule received about ten bundles (some of which may be branches of a smaller number, starting from the pedicel), and that these were increased, higher up in the cupule, by further branching.

We have now to consider the evidence as to the structure of the bundles, and will begin with that of the pedicel. Perhaps the most important section from this point of view is that illustrated in Plate 8, figs. 9 and 10 (U. C. L., R. 15). This section, as a whole, appears to be a tangential one through the pedicel and part of the cupule. Two of the characteristic glands are seen, one of which is *in situ*, leaving no doubt as to the identification with *Lagenostoma Lomaxi* or some closely similar form. The seed is absent, but appears to have been originally attached to the tissue marked *a*, as shown by the vertically elongated cells at this point, which exactly agree with those at the base of the seed in other specimens (*cf.* photos. 5 and 16, and fig. 33 from W. 1930 and S. 558). The part lying directly below the seed-base would thus be the pedicel; on the right, one side of the cupule is seen in position; the detached piece above may either be the left-hand side of the cupule displaced, or the distal part of the right-hand side, but the point is of little importance. The resemblance of the whole to the pedicel and cupule, as shown in S. 558 (phot. 16 and fig. 33), supposing the seed detached, is striking. Two bundles passing out to the cupule are

seen at the top of the pedicel (fig. 9, *v.b.*'), one in transverse, the other in longitudinal section ; other strands traverse the cupule itself.

The pedicel, measured from the seed-base to its lower termination, is about 1·5 millims. in length, but is probably incomplete. The most important feature is the presence of a large vascular bundle, seen in somewhat oblique transverse section, near the lower end of the pedicel. This bundle, shown in detail in fig. 10, has a roughly triangular or three-lobed section ; the maximum diameter of the xylem is about 300μ . The tracheides are cut obliquely, showing scalariform, or at some places pitted walls; they are commonly about 25μ in diameter, but some are much smaller, down to about 12μ . At three or four points there are gaps in the interior of the xylem, where the tissue has partly perished. These gaps were probably filled by parenchyma ; in some there seem to be remains of disorganised tracheides. The smaller tracheides of the bundle border on the gaps, some or all of which probably represent the position of the protoxylem. That the latter was internal appears certain, for the peripheral elements are generally scalariform tracheides, of comparatively large size, and with no signs of disorganisation. The structure thus indicates that the bundle was a mesarch one ; it was also, to all appearance, concentric, though the phloëm region is too badly preserved to show any details. The bundle resembles that in a small rachis of *Lyginodendron Oldhamium* more nearly than any other form of vascular strand met with in these petrifications (*cf.* fig. 10 with Plate 6, phot. 27, from the rachis of *Lyginodendron*).

There can be little doubt that the bundle just described was that of the pedicel, which must have been bent at a considerable angle, so as to be cut somewhat transversely below, while seen in nearly longitudinal section in its upper part. The bundle corresponds with the large strand (*a*), seen in longitudinal section in U. C. L., R. 14, *a* (fig. 11), both in dimensions (diameter about 300μ in each), and structure. The tracheides are similar, and in the longitudinal section parenchyma occurs in the xylem, answering to the gaps in the less well-preserved transverse section. The bundle of the pedicel in S. 558 also agrees in structure, but its dimensions are much less, the xylem being about 150μ in diameter. It is probable, however, that this section is not median ; the apparent diameter of the strand agrees very nearly with that of one of the projecting lobes of the xylem in U. C. L., R. 15.*

The anatomy of the pedicel is of considerable importance, as indicating that the organ on which the cupule and seed were borne was of a foliar nature. The structure is that of a petiole or rachis and not of a stem or branch.

* Another somewhat fragmentary longitudinal section of the pedicel occurs in section, U. C. L., R. 14, *b*. This may belong to the cupule of which portions are shown in the same slide and in the adjacent section, U. C. L., R. 14, *a*. It was clearly desirable to obtain a truly transverse section of the pedicel, and a search was made for the section next below the transverse series of three, often referred to above. Several sections from the same series were found ; the only one which appears to come below the seed is in the Manchester Museum Collection, K₂. 14259. Several fragments of cupular tissue of *L. Lomari* are present, one of which contains a bundle not unlike that in U. C. L., R. 14, *a*, but smaller (175μ maximum diameter). It could not be referred with certainty to the pedicel.

The structure of the bundles in the cupule is fairly shown in several sections. Fig. 15 represents a transverse section of a bundle in a detached piece of cupule (shown in Plate 8, fig. 14) in U. C. L., R. 14, A., probably a fragment of the specimen shown in tangential section in the same slide (fig. 11). The structure of the bundle is to all appearance collateral; the small-celled tissue which alone can represent the phloëm is limited to one side of the strand; on the opposite side the parenchyma abuts immediately on the wood. The same collateral structure is shown in other preparations, *e.g.*, W. 1915, M. and O. (fig. 16), from the series of three.

In the section represented in fig. 15, the orientation is inverted, the phloëm facing almost directly inwards. In most other cases, especially in the transverse series of three, the indications point to normal orientation (see fig. 16). The orientation may have really varied, perhaps in relation to the branching of the bundles, or the exceptional cases may be due to some displacement.

The evidence, though far from clear, owing to imperfect preservation, goes to show that the smaller cupular bundles at any rate were collateral, and in the majority of cases observed had normal orientation. In one or two cases the larger bundles of the cupule appear to have retained concentric structure.

The transverse section in fig. 15 does not clearly show the position of the protoxylem. In other sections, however (*e.g.*, fig. 16, from W. 1915, O.), the smallest elements are almost always found near the middle of the xylem; in the finer strands they sometimes approach one or the other surface, but the mesarch arrangement is the rule. The longitudinal sections sometimes clearly show narrow spiral elements in the interior of the xylem (fig. 12) confirming the position of the protoxylem, as indicated in transverse sections. The tracheides are for the most part spiral or scalariform (fig. 12). Here and there, however, especially in the larger strands, elements with multiseriate bordered pits occur (see fig. 13 from the bundle *b* shown in fig. 11). These pitted elements exactly resemble those characteristic of *Lyginodendron Oldhamium*, and it is significant that in the foliar organs of that plant, just as in the cupule of *Lagenostoma Lomaxi*, spiral and scalariform tracheides preponderate, while the pitted elements, so general in the stem, are comparatively rare. In the finer strands of the lamina in *Lyginodendron* the pitted tracheides are wanting, and this seems to hold good for the finer cupular bundles of our *Lagenostoma*.

The vascular bundles of the cupule are enclosed in a conspicuous sheath, of large, rather thin-walled cells (see figs. 12 and 15) as much as 50μ in radial diameter. In this respect, again, they agree with the bundles in the leaflets of *Lyginodendron*, where the large-celled sheath is likewise a striking feature.* So far as comparison is possible the bundles in the cupule of *Lagenostoma* thus agree in all respects with those in the leaflets of *Lyginodendron*, while, as we have seen, the main strand of the pedicel in the former closely resembles that of the vegetative rachis in the latter.

As regards the parenchyma of the cupule there is little to be said; its preservation

* WILLIAMSON and SCOTT, "Lyginodendron and *Heterangium*," *loc. cit.*, p. 731; Plate 24, fig. 16.

is always bad, even in the youngest specimens (see fig. 34, U. C. L., R. 13); the tissue between the bundles is reduced to a brown disorganised mass, in which mere traces of the cellular structure are recognisable. The peripheral zone is somewhat better preserved, and appears to consist of two or three layers of elongated elements, with walls rather thicker than those of the subjacent tissue. This darker zone sometimes contrasts rather sharply with the light brown of the disorganised parenchyma within (see figs. 1, 2 and 9). Elements with black contents, recalling the "secretory sacs" of *Lyginodendron*, can sometimes be detected in the cupular tissue, but their characters are not definite enough to help materially in identification. The most interesting point about the ground-tissue of the cupule is the fact that it was infested with fungi. Fungus-spores are almost always to be detected; in some specimens (e.g., U. C. L., R. 15) the tissues are completely filled with them, and they occur in such masses that they might be taken for a part of the normal structure, if it were not for comparison with other specimens in which the same bodies occur isolated. Fungal hyphae are also found, sometimes forming dense strands following the course of the vascular bundles. All indications point to the cupule having already been an effete organ at the stage when its preservation took place, its condition contrasts markedly with that of the well-preserved adjacent fragments of the vegetative organs of *Lyginodendron* and other plants. This fact has an important bearing on the condition of the cupular glands, now to be described.

The glands form the most conspicuous feature of the cupule, by means of which even small fragments can usually be recognised at once; they occur on all parts of the cupule and pedicel (phot. 1, 4 and 15, figs. 1-3, 7 and 11) and are very numerous. Thus in the transverse section represented in fig. 7 no less than twenty-three are shown *in situ*.

The glands are massive structures, seated with a broad base on the cupule; sometimes they are practically sessile, but usually there is a distinct stalk, varying much in length (see phot. 1, 4, 16, 21 and 22, figs. 7, 14 and 17). In all cases the free end of the gland is formed by a large, more or less spherical head. In dimensions the head of the gland ranges from about $160-260\mu$ in diameter. The length of the gland as a whole varies much; the longest observed was 1.2 millims. in length (fig. 17), while the stalk was 600μ thick at the base, diminishing to 120μ at the narrowest part, just below the head, which was here 220μ in diameter. As a rule the stalk is short—not much exceeding the diameter of the head—and sometimes there is no recognisable stalk at all, the spherical head being seated directly on the surface of the cupule (fig. 7).

The head of the cupular gland is in all cases a hollow structure; the shell of tissue enclosing the cavity is one cell thick at the free end, increasing to two cells or more at the sides, as the stalk is approached (see fig. 17 and phot. 21). The cavity is, as a rule, quite empty; at most only slight remains of disorganised tissue are found within it. The clearest case is that shown in phot. 23, where two or three fairly

definite cell-like bodies are seen inside the head ; they are probably not cells, but may represent the remnant of a broken-down tissue. Occasionally there are slight indications (from differences in colour) of the presence of some structureless organic substance within the gland. The cavity, as a rule, is approximately spherical, but sometimes it has an obovate or pear-shaped contour (see phot. 22) ; this may depend on the less complete disappearance of the internal tissue.

The stalk, when present, is a solid column of tissue many cells thick. It is never found well preserved, but a peripheral zone of elongated, apparently thick-walled cells, continuous with the outer layer of the cupule, can sometimes be distinguished (phot. 21 and fig. 17). The form of the internal cells of the stalk is obscure, owing to the state of preservation, but seems to have varied with that of the gland as a whole, the cells being more elongated in the longer stalks. Where the gland is sessile, the wall of the head gradually thickens towards the base, and passes over directly into the adjacent tissue of the cupule.

No trace of a vascular supply has been found in connection with any of the glands.

In a few cases the tissue of the head or stalk has been thrown into spiny elevations, no doubt by unequal contraction of the inner and outer layers.

The structure of the cupular glands will be further considered in the next section, where they are compared with those occurring on the vegetative organs of *Lyginodendron*.

Not uncommonly, multicellular hairs occur on the cupule ; several are present, for example, on the specimen shown in transverse section in fig. 7. They are most conspicuous, however, on the cupule of the young seed or ovule (U. C. L., R. 13) represented in fig. 34, where they occur in abundance on a long lobe of the cupule, forming a conspicuous tuft at its extremity (*h*). On the older cupules they are but sparsely present ; probably they belonged to the young condition of the organ, and were shed as it advanced in age. The hairs are cylindrical structures (fig. 8), consisting of a single row of three or four cells, or perhaps more, for they are rarely seen complete. The cells are about 20μ in diameter, and range in length from about $30-60\mu$.

Summary of Cupule.

The chief facts with regard to the cupule of *Lagenostoma Lomaxi* may be briefly summed up as follows :—

The young seed was enclosed in a cupule or envelope exceeding the seed in length. Mature seeds are sometimes found still within the cupule, but are more often free.

The cupule was borne terminally on a pedicel ; it formed a continuous ribbed cup below, and divided above into a number of lobes or segments.

The pedicel contained a single vascular bundle, which, before entering the chalaza, gave off numerous branches into the cupule, traversing it throughout its length and extending into the segments.

The bundle of the pedicel appears to have had a concentric mesarch structure, while its branches in the cupule became collateral, the orientation, in the majority of cases, being normal.

Large and prominent multicellular glands of capitate form were borne on the cupule and pedicel; the head of the gland, in the usual state of preservation, is hollow.

Uniseriate hairs were also borne on the cupule, and are chiefly found on the younger specimens.

COMPARISON WITH THE VEGETATIVE ORGANS OF *Lyginodendron*.

The first and most important point to be considered is the comparison of the glands, for it was the resemblance between the glands occurring on the cupule of *Lagenostoma Lomaxi* and those already known on the vegetative parts of *Lyginodendron* which first suggested a connection between these fossils.

The characteristic cortical emergences, which form a constant feature of the stem and leaves of *Lyginodendron Oldhamium*, have been familiar since WILLIAMSON first described them in 1890.* Glandular outgrowths, however, do not seem to have been distinguished till a few years later, in 1895.† They are by no means equally frequent in all specimens; in some of the material they may long be sought in vain, while in other cases they are extremely abundant, and are met with in practically every section of the stem or leaf. The form of *Lyginodendron* occurring at Dulesgate, with which the specimens of *Lagenostoma Lomaxi* are closely associated, is exceptionally rich in glands. They are present alike on stem, petiole and rachis, and on the leaflets themselves. These vegetative glands are massive capitate structures, usually with a stalk of varying length, but occasionally sessile.

The largest glands generally occur on the stem. The gland shown in Plate 8, fig. 18, borne on the cortex of a stem, evidently of a considerable size, may serve as a fair example of the long-stalked form. Here the whole length is 2·2 millims.; the stalk is about 700μ thick at the base, and about 200μ in the upper part, the head having a diameter of about 300μ . On other stems, glands as much as 3 millims. in length have been observed, but most of the stem-glands are much shorter. The longer glands seem to have easily become detached, for isolated specimens, exactly agreeing with those found elsewhere in connection with the stem, are common in the Dulesgate material, where they occur mixed up with the seeds of *Lagenostoma Lomaxi*. On the petiole and rachis the long type of gland is comparatively rare, though here also a length of as much as 2 millims. is sometimes reached. Usually the petiolar glands

* "Organisation of Fossil Plants of Coal-measures, Part XVII.," 'Phil. Trans.,' B, vol. 181 (1890), p. 90, figs. 1, 6, 7, 8, and 9.

† WILLIAMSON and SCOTT, "Further Observations on the Organisation of Fossil Plants, &c., Part III.," 'Phil. Trans.,' B, vol. 186 (1895), p. 730, Plate 23, fig. 12.

are short—about 300 – 400μ in length—with heads varying from about 160 – 240μ in diameter; sometimes the glands are sessile, and this is commonly the case where they are found on the pinnules of the leaf.

We have seen above (p. 223) that the cupular glands of *Lagenostoma Lomaxi* may attain a length of $1\cdot2$ millim., but are more commonly short, ranging usually from a total length of about 500μ down to the sessile form, while the diameter of the head varies from about 160 – 260μ . Thus the dimensions of the cupular glands are practically identical with those of the vegetative glands, the agreement being most exact with the glands that occur on the petiole and rachis of the leaf. The form is also the same, and shows about the same range of variation (compare, for example, phot. 16 from a cupule with phot. 19 from a petiole).

The structure of the vegetative glands is well exhibited in many specimens, as shown in Plate 6, photos. 24–26, and in Plate 8, fig. 18. Their preservation is generally far more perfect than that of the cupular glands. A particularly good example is represented in phot. 24, from a detached gland, occurring in the same block from Dulesgate which yielded most of the specimens of the seed. It is a long gland ($1\cdot2$ millims. in total length) with the head of the maximum dimensions, about 400μ in diameter; it was probably borne on the stem, as it agrees closely with glands found *in situ* on stems of *Lyginodendron* from the same locality.

The interior of the head is occupied by a mass of small cells, which we regard as constituting the secretory tissue of the organ. The general shape of the secretory mass is obovate; the cells are for the most part perfect, but some larger lumina in the lower part of the group, may indicate that here a lysigenetic process was beginning. At the free end the boundary wall of the head is formed by a single layer of narrow cells; lower down the wall increases in thickness, especially on one side, as regards both the number and width of its cells. The stalk is bounded throughout by a well-marked epidermis of somewhat elongated cells; the depression near the base (*st.* in phot. 24) no doubt indicates the position of a stoma. The internal tissue of the stalk consists in the upper part of elongated cells, while towards the base the elements are shorter; the thickness of the cell walls diminishes from without inwards. Dark coloured cells scattered in the internal tissues resemble the “secretory sacs” of the stem and petiole.

Essentially the same structure is shown in the long gland from the stem, represented in fig. 18, and, generally, all the vegetative glands in question exhibit the same features,* apart from insignificant variations. Where the gland as a whole is short the cells of the stalk are usually short (also see phot. 20). In no case was any sign of a vascular strand observed in connection with a gland.

Allowing for the inferior preservation of the cupule of *Lagenostoma Lomaxi* as compared with that of the vegetative organs of *Lyginodendron*, it is evident that the

* On some stems much smaller and simpler gland-like bodies occur side by side with those described. They do not affect the present question and will be dealt with on another occasion.

glands of the one agree very closely with those of the other. In dimensions and form, and in the structure of the stalk, there is in fact no distinction to be drawn between them. As regards most of the specimens, however, there is this difference: in all cupular glands observed the head is empty, or very nearly so, while in the great majority of vegetative glands it is filled with a small-celled tissue, usually well-preserved. So long as this difference proved constant it was impossible to regard the two organs as identical. On searching, however, through large numbers of sections of *Lyginodendron*, cases were soon met with in which the vegetative glands were in the same condition as those on the cupule of the *Lagenostoma*. The first instance of this was observed in slides 1915 B. and 1415 C. of the WILLIAMSON Collection, cut from the same block from which most of the specimens of the seed were derived. A small rachis, about 2 millims. in maximum diameter, with the typical *Lyginodendron* structure, appears in each of these sections; it bears glands of the usual vegetative type, but with the head completely hollow, just as in the cupular glands.* In the two sections three of these hollow glands are shown. The clearest of the three has a length of 320μ , with the head 190μ in diameter. Subsequently, an even better instance of the hollow state of preservation of vegetative glands was found. The specimen is a petiole or rachis of *Lyginodendron*, measuring about 4×2 millims. in transverse section. One section is in D. H. SCOTT'S Collection (S. 625) and four others are in the collection at University College (U. C. L., M. 11, *a-d*).

It was from this specimen that the illustrations (phot. 18, 19 and 20) were taken. A large number of glands are present, and in all those in which the head is shown, of which there are eleven in the three sections particularly studied, its cavity is perfectly empty. The glands vary in size; that shown in phot. 20 is among the largest, it measures 400μ in total length and the head is about 240μ in diameter. The agreement with the cupular glands is strikingly exact, as shown, for example, on comparing phot. 20, from the petiole, with phot. 21, from the cupule; both photographs are on the same scale. In some of these vegetative glands (phot. 20) the tissue of the stalk is completely preserved, as is usually the case in the cupular glands.

We thus find that the vegetative glands of *Lyginodendron*, when in a certain condition of preservation,† agree in all points with those on the cupule of *Lagenostoma Lomaxi*. It is probable that the hollow state of the head in these glands is due to the breaking down of secretory tissue during life, rather than to *post-mortem* decay. Intermediate conditions are sometimes found in the vegetative glands. In the specimen shown in phot. 25, for example, the secretory tissue is beginning to show signs of disorganisation, and where this is the case there is some resemblance to the fragments of broken-down tissue seen in the cupular gland represented in phot. 23. In several vegetative glands (see phot. 26) a definite gap had formed in the middle of the secretory mass. We thus see that there is a series of cases connecting the

* The authors are indebted to Miss M. C. STOPES for the detection of this valuable piece of evidence.

† Additional examples of this state of preservation have since come under observation. June 25, 1904.

hollow gland characteristic of the cupule, with the fully preserved condition which is more usual on the vegetative organs.

The fact that the cupular glands are almost always found with the head empty is no doubt to be explained by the effete condition of the cupule at the time it was preserved, as indicated by the state of all its tissues. Its functional activity must have been limited to a stage earlier than any which has as yet come under observation, though in its old age it may still have served as a protective husk. So far as the glands are concerned, the agreement between the cupule of *Lagenostoma Lomaxi* and the vegetative organs of *Lyginodendron Oldhamium* is thus found to be complete. No other fossil plant is known which bears glands at all comparable to those described.

As regards the vascular system, the main points of comparison have already been indicated and may be shortly recapitulated here. The vascular bundle of the pedicel in *Lagenostoma Lomaxi* agrees in form, and in its mesarch and to all appearance concentric structure, with the bundle of a small petiole or rachis in *Lyginodendron Oldhamium* (see Plate 8, fig. 10 and compare Plate 6, phot. 27).

The bundles of the cupule of *Lagenostoma* are usually assuming collateral structure with mesarch xylem, agree with those in the pinnules of *Lyginodendron*. They further correspond in possessing a conspicuous, large-celled bundle-sheath. In the smaller strands of the cupule only spiral and scalariform elements are found, while in the main strand of the pedicel and the bundles immediately springing from it, elements with multiseriate bordered pits also occur. In these respects, again, there is an exact agreement with the bundles of the leaflets and rachis respectively of *Lyginodendron*. The evidence from the vascular structure thus completely confirms the attribution first suggested by a comparison of the glands.

The preservation of the other tissues of the cupule is not sufficiently good to admit of any profitable comparison with the vegetative organs. The moribund condition of the cupule, as indicated by the constant presence of fungal spores and hyphae, sufficiently accounts for its inferior state of preservation as compared with that of the foliage leaves of *Lyginodendron*.

The comparison between the structure of *Lagenostoma Lomaxi* and that of *Lyginodendron* has been based entirely on the cupule and pedicel of the former. The seed itself is so highly specialised an organ that no detailed agreement with vegetative structures is to be looked for. At the same time, there is certainly no discrepancy. It may be mentioned in this connection that in the closely allied *Lagenostoma ovoides* "secretory sacs," resembling those of *Lyginodendron*, have been observed by one of us in the parenchyma filling the loculi of the canopy.

It must be remembered that the argument from detailed correspondence of structure is strengthened by that from intimate association. Evidence of the latter kind, though worthless by itself, is by no means without weight as an auxiliary to the former. The specimens of *Lagenostoma Lomaxi* everywhere occur mixed up with the

stems, leaves, and roots of *Lyginodendron Oldhamium*, and it is with the peculiarly glandular form of the "species" that the seeds, with their glandular cupules, are associated.* Where vegetative and reproductive organs presenting identical structural features, not known to occur in other plants, are thus found in close and constant association, the inference that the one belonged to the other appears irresistible. Evidence from actual continuity is always the final goal in questions of attribution among fossil plants; the seed of *Lagenostoma Lomaxi* has not yet been found *in situ* on the *Lyginodendron* plant, but short of this the evidence for the one belonging to the other could scarcely be stronger than it is.

THE POSITION OF THE SEED ON THE PLANT.

Until the seed has been found in actual connection with the plant to which it belonged, we are necessarily left without any direct evidence as to how the fructification was borne. As already pointed out, the anatomical evidence clearly indicates that the cupule together with the pedicel was of a foliar nature. This foliar organ may represent either an entire sporophyll, borne with its fellows on some axial structure, or a modified pinnule of a compound leaf, corresponding to the sterile foliage of the plant. Either interpretation is possible.

Thanks to Mr. LOMAX's observations we now know that the stem of *Lyginodendron* was branched;† in some forms of the plant the ramification was many times repeated, and it is possible that some of the ultimate branches may have assumed the character of floral axes, though we have as yet no evidence that this was the case. The peculiar "bud-like structure" described in 1895‡ might be thought of in this connection. A number of specimens of the same nature have come to light since this description was published, and a series of sections recently received from Mr. LOMAX shows conclusively that the "bud-like structure," in some cases at all events, was nothing but a very young stem or branch, densely clothed with long and often glandular emergences. There is also evidence that similar young or arrested branches occasionally occurred in the axils of the leaves on the largest stems. At present, however, there is nothing to show that any of these branches were connected with reproduction.

It is unlikely in any case that a definite strobilus was formed; the radial symmetry of the seed and cupule and the absence of any signs of mutual compression indicate that the fructification—whatever its morphological nature—was a lax one.

The alternative hypothesis, that the seeds were borne on the frond, is at least

* In one case a leaflet of *Lyginodendron* is found enclosed within the cupule of a seed. See phot. 4 (W. 1931).

† J. LOMAX, "Some New Features in Relation to *Lyginodendron Oldhamium*," 'Annals of Botany,' vol. 16, December, 1902.

‡ WILLIAMSON and SCOTT, *loc. cit.*, p. 732, Plate 24, figs. 14 and 15.

equally probable, though for this also we have no direct evidence; no structures suggesting fertile fronds or fertile pinnæ have as yet been detected in the petrified specimens of *Lyginodendron*. The very abundant and often well-preserved foliage appears to have been all of the familiar sterile type. Nor, so far as we are aware, has *Sphenopteris Höninghausi*, which is identical with the foliage of *Lyginodendron* preserved in the form of impressions, been found as yet in any but the sterile form. STUR, however, has attributed certain fertile pinnæ to the closely similar species *Sphenopteris Stangeri*, of lower carboniferous age, and probably this attribution is correct, though evidence from actual continuity is wanting. The fructification borne on the fertile pinnæ is *Calymmatotheca Stangeri*.* If *Calymmatotheca Stangeri* belonged to a *Lyginodendron*, as appears probable, it may possibly represent the male fructification of the plant (see below, p. 238). It would, even in that case, however, establish a certain presumption that the female reproductive bodies might have been borne in a similar way on the frond.

Mr. KIDSTON's important discovery of the seeds of *Neuropteris heterophylla*,† announced during the writing of the present paper, shows that in this member of Cycadofilices the seed was borne on a pinna of the frond. The position is apparently terminal, but may have been lateral originally. The analogy of this plant, though not belonging immediately to the same family as *Lyginodendron*, no doubt somewhat increases the probability that the seeds were borne on the frond in the latter genus. A further analogy may perhaps be found in a fossil about to be described by Mr. ARBER in conjunction with one of the present writers, where there is reason to suspect that the numerous *Lagenostoma*-like seeds may have belonged to the rachis associated with them, possibly a fertile frond of the *Sphenopteris* type. Other specimens, showing seeds *in situ*, point in the same direction.

It is possible that among recent Ferns the ancient and now monotypic genus *Thyrsopteris* may give us the best idea how the fructification of *Lyginodendron* was borne. Here the branched fertile pinnæ, springing from the main rachis of the frond, terminate in the sori, each surrounded by its cupule-like indusium; in the Palæozoic plant similar branched pinnæ may have borne sometimes the cupulate seeds, sometimes the pollen-bearing sporangia. On this view the pedicel of our *Lagenostoma* would represent an ultimate ramification of the fertile rachis.

MORPHOLOGY.

In its whole organisation *Lagenostoma Lomaxi* recalls so vividly the seed of a modern Cycad that it is unnecessary here to do more than recapitulate, in the briefest way, the characters which mark it out for inclusion in the class of structures termed seeds.

* STUR, "Die Culmflora," 'Abhandl. K. K. Geol. Reichsanstalt' (Vienna), vol. 8, 1877.

† "On the Fructification of *Neuropteris heterophylla*, BRONGNT.," read before the Royal Society on December 3, 1903 ('Phil. Trans.', B, vol. 197, p. 1).

Lagenostoma has an integument with micropyle, and there is a permanently enclosed megasporangium containing a prothallium. Pollination no doubt took place on the parent plant, and the structure was then detached as a whole through the agency of the layer of separation.

In the extrusion of mucilage from its integument *Lagenostoma Lomaxi* recalls an adaptation widely prevalent among the seeds of higher plants; an adaptation which though trifling in itself, helps to confirm the belief that the integument had already become an integral portion of the seed.

The main point in which *Lagenostoma* diverges from the typical seed is in the lack of an embryo, a negative character common to the whole series of fossil Gymnospermous seeds that have been recovered from the Palæozoic rocks. This point is discussed elsewhere in the present paper and need not be pursued here. These earlier seed-types perhaps retained the Fern-like mode of continuous development from the fertilised egg-cell to the exclusion of any definite resting period such as we usually associate with a "ripe seed." If any pause occurred it may perhaps have immediately preceded fertilisation and have coincided with the maturing of the microspores in the pollen-chamber and the liberation of spermatozoids. This interpretation, too, seems consistent with the processes as we know them in living Pteridophytes.

The seed of *Lyginodendron* differed from recent seeds in the early maturing of its tissues. Already before fertilisation has taken place they appear to have reached the limits of their development, and would be incapable of further stretching. The ovular stage, *i.e.*, the persistence of an embryonic condition of the tissues of nucellus and integument till after fertilisation had occurred, was a later adaptation.

There is another feature in which our seed is peculiar amongst the known seeds of this period. The micropyle is the pore of access to the nucellus, and in other seeds the microspores must needs traverse it on the way to effect a lodgment in the pollen-chamber. Here, this is unnecessary, seeing that the micropyle is disposed as a collar around a pollen-chamber whose orifice communicates directly with the outside.* The integument covers the seed, leaving exposed the spot appropriated to the reception of the pollen. It is possible we have in this feature a reminiscence of the pollination of an ancestral naked megasporangium.

We may pass on now to a consideration of the homologies of the several parts of the seed and of the enclosing cupule. The modified apex of the nucellus, the pollen-chamber, is even more highly specialised than the corresponding structure among the Cycads. For the bell-shaped, crevice-like form of the cavity in *Lagenostoma* connotes a relatively high degree of precision in the movements of the spermatozoids, and affords ground for the suspicion that the distribution of the archegonia will be found

* A similar relation obtains in the genus *Araucaria*, *cf.* STRASBURGER, 'Die Coniferen und die Gnetaceen,' p. 65 and Plate 7, fig. 56. The same appears to hold good for *Sequoia*; LAWSON, *Gametophytes, &c.*, of *Sequoia sempervirens*, 'Ann. of Bot.,' vol. 18, January, 1904, p. 6.

to have a similar relation. Efficiency in the primitive types of seeds seems to have depended on the perfection of the pollen-chamber. Later came an advance from the side of the microspore; the pollen-tube was evolved, and upon its appearance followed the decline of the pollen-chamber.*

Under the circumstances it is hardly to be expected that the pollen-chamber of *Lagenostoma* should offer any evident indication of the manner of its origination from a Fern sporangium.

The peculiar integument of the seed demands some consideration. Distally it consists of the chambered canopy which freely surrounds the apex of the nucellus, whilst proximally it is coalescent with the lower four-fifths of the seed. It was a vascular structure, supplied with bundles from the vascular strand that entered at the chalaza. These bundles, as they run in the wall of the seed, lie well within the integumental region, as defined by continuing backwards the actual plane of separation of nucellus and integument. There can be no question in this case of a nucellar origin of the bundles.

The second point to be noted is that of the possible multiple character of the integument in its free part, as suggested by the chambering of the canopy. In *Lagenostoma Lomaxi* the several loculi of the canopy are as completely fused with one another as are the carpels in a syncarpous gynæceum, though, of course, near its insertion the lining of the canopy is evidently grooved, and even where the grooves disappear, giving place to radial septa, indications of the double origin of the septa are still discernible for some distance. Taken in conjunction with WILLIAMSON'S *Lagenostoma physoides*,† a seed still under re-investigation, in which the canopy seems to be represented by a whorl of free tentacles inserted below and enfolding the pollen-chamber, a multiple origin for the integument would appear not improbable.

The outer envelope of the seed, the cupule, is, of course, a much less specialised organ than the integument, and, as we have shown, has much in common with the ordinary vegetative pinnules of *Lyginodendron*.

Translated into appropriate Filicinean terminology, we have in *Lagenostoma* a megasporangium which has been enclosed in two successive, concentric, indusium-like structures, of which the inner has become an integral portion of a new organ, the seed. The outer is probably of later origin, and would appear to have afforded protection to the seed only when the latter was quite young. It is quite possible that the two enclosures have originated very similarly, *i.e.*, as peltate, lobed structures, and that the present integument was once a comparatively unspecialised cupule-like indusium. An exact parallel is hardly to be found among recent Ferns, though a certain analogy is offered by the case of *Onoclea sensibilis*, in which each sorus is enclosed by its own proper indusium as well as by an infolded marginal lobe of the pinnule. *Azolla*, too, may be cited in this connection. In this genus the sori—each

* Cf. 'Annals of Botany,' vol. 17, p. 452.

† WILLIAMSON, "On the Organisation, &c., Part VIII.," 'Phil. Trans.,' vol. 167, fig. 77.

with its own close-fitting indusium—are inserted in pairs upon the ventral lobe of the sporophyll, while from the base of the dorsal lobe a general sheath, or "involucre," is provided, which forms an enclosure for the group of sori.*

In the present state of our knowledge the term *indusium* carries no very precise morphological signification, and conflicting views have been expressed as to its origin and nature. In such groups of the Polypodiaceæ, however, as *Dicksonieæ* and *Davillieæ*, the ontogenetic indications are consistent with a marginal or terminal origin for the sorus, whilst the indusium has arisen from more or less connate marginal outgrowths, which form a theca around the sorus. The relations in *Lagenostoma* appear to justify a comparison with the groups cited, whilst the Hymenophyllaceæ offer a further parallel. That the enclosures of *Lagenostoma* should retain their vascular strands, whilst the indusia in most Ferns are non-vascular, is no bar to the existence of a homology between these structures. In the great majority of cases a flimsy, reduced structure is best adapted to the discharge of its functions by a Fern indusium, though instances occur in which the indusium is penetrated by vascular bundles.†

In *Lagenostoma*, on the other hand, special reasons may exist for the retention of the bundles. Reference has already been made to a possible function of these strands in the canopy (see p. 214); whilst in the cupule, which is richly vascular, there is, of course, the secretory function of the numerous glands.

The cupule may be regarded as a comparatively new structure, dating its origin, perhaps, from the time when the seed habit was acquired, and the old or primary indusium (the canopy) became incorporated as an integral portion of the seed.

We have heard with much interest and appreciation of the views of Miss M. BENSON upon the homologies of this seed.‡ Following PRANTL,§ this botanist regards the seed as the equivalent of a sorus, but, unlike PRANTL, she interprets the integument (the canopy of *Lagenostoma*) as a reduced or sterilised series of sporangia. The seed, as a whole, is regarded as a metamorphosed synangium, of which the central sporangium alone retains its pristine function.||

We turn now to a consideration of the possible relations of the more primitive Gymnospermous seeds to *Lagenostoma*.

First, we would cite *Gnetopsis elliptica*,¶ from the French Permo-carboniferous of Grand' Croix. This is the only known fossil seed possessing a cupule, though in this

* GOEBEL, 'Organographie,' pp. 669, 670.

† PRANTL, 'Unters. zur Morphologie d. Gefässkryptogamen,' Heft 1, 'Die Hymenophyllaceen,' pp. 36, 37, and fig. 97.

‡ M. BENSON, 'Ann. of Bot.,' vol. 18, p. 161, January, 1904.

§ PRANTL, 'Unters. zur Morphologie d. Gefässkryptogamen,' Heft 2, 'Die Schizæaceen,' p. 153.

|| It would unduly prolong the present paper to enter here on any discussion of this important suggestion, which has been published since our memoir was communicated to the Royal Society.

¶ Cf. RENAULT, 'Cours de Bot. Fossile,' vol. 4, p. 180, Plate 20, 1885.

case the relations differ from *Lagenostoma* in that the cupule contained as many as four seeds. This seed, like our own, shows indications of a complicated integument, which suggests comparison with the canopy. The pollen-chamber, also, seems to have possessed a central cone not unlike the one we have described. Whatever may have been the plant that bore this seed, the analogies which the latter presents with *Lagenostoma* are most striking.

Amongst existing Gymnosperms, the Taxaceæ at once recall the *Lagenostoma* condition in the frequent possession of a second integument (aril). In *Taxus* and *Phyllocladus* the aril is still free from the seed; in *Torreya* it is adnate throughout the greater portion of the seed, whilst in *Cephalotaxus* it may possibly be represented by the outer fleshy covering of the testa.

At present it is undesirable to press these comparisons too closely. The suggestions made are tentative and provisional, and may need revision, as further additions to our knowledge of the mode of fructification of the Cycadofilices accrue.

A comparison of the seeds of Cycads with *Lagenostoma* is inevitable. The vegetative organs of *Lyginodendron* possess marked Cycadean features, whilst the seed, which we attribute to this fossil, has an essentially Cycadean organisation. The canopy of a *Lagenostoma* may well have undergone simplification into the hard integument of a Cycadean seed, and, in that case, the vascular strands, which run in or near the plane of union of nucellus and integument in the latter, should correspond with the integumental bundles of *Lagenostoma*, even though they no longer pass into the free part of the integument.

Whether the fleshy sarcotesta of *Cycas*, with its vascular strands, correspond to a completely adnate cupule, may, perhaps, be left an open question. In any case, the detailed structure of Cycadean seeds is a subject fully deserving further attention and elucidation.

THE SYSTEMATIC POSITION OF *Lyginodendron*.

When BINNEY, in 1866, first described his newly-discovered *Dadoxylon Oldhamium*, no doubt of the Gymnospermous affinities of the plant seems to have occurred to the mind of its discoverer. "It evidently belonged," he says, "to the genus *Pinites* of WITHAM, since changed by ENDLICHER and BRONGNIART into *Dadoxylon*."^{*} WILLIAMSON's full investigation of the structure of the stem, published in 1873,[†] left the taxonomic relations of the plant doubtful, but removed it definitely from the *Dadoxylon* lumber-room; WILLIAMSON had, in fact, already separated it in 1869, under the generic name *Dictyoxylon*.[‡] Speaking of *Lyginodendron Oldhamium*,

* BINNEY, "On Fossil Wood in Calcareous Nodules found in the Upper Foot Coal, near Oldham," 'Lit. and Phil. Soc. Proc.,' Manchester, vol. 56, p. 113, read February 20, 1866. BINNEY, however, compared the primary wood of his stem to that of *Sigillaria elegans*.

† "Organisation of Fossil Plants of Coal-measures, Part IV.," 'Phil. Trans.,' 1873.

‡ "On the Structure and Affinities of some Exogenous Stems from the Coal-measures," 'Monthly Microscopical Journal,' vol. 2, p. 66, 1869.

as he named BINNEY's plant in 1873 for the first time, and of the allied *Heterangium Grievii*, WILLIAMSON says: "The question of the botanical position of both the above plants remains undecided, and I confess I shrink from arriving at a decision in the present state of our knowledge respecting them. If I succeed in establishing a connection between the common Oldham plant and the equally common *Edraxylon* [*Rachiopteris aspera*, of later memoirs], then, strange as it may appear, the former will become an undoubted arborescent Fern; at the same time, it has many features of affinity with the Lycopodiaceæ that must not be overlooked."* He goes on to speak of the difficulty of distinguishing between the fossil stems of Lycopods and Ferns, but adds, in a footnote, that more recent researches had rendered it increasingly probable that *Heterangium Grievii* was a true Fern. He always recognised the close affinity between the two genera, an opinion which more recent work has all tended to confirm.

It is remarkable that WILLIAMSON at that time seems only to have hesitated between Lycopods and Ferns, and to have lost sight for the moment of the indications of Gymnospermous affinity which these plants present. Perhaps this was a natural reaction against BINNEY's too confident reference of the Oldham plant to *Dadoxylon*.

In his memoir of 1874,† WILLIAMSON described *Rachiopteris aspera*, as he now called the petiole previously named *Edraxylon*, and compared it with certain Fern-fronds known as impressions, *Sphenopteris Höninghausi*, BRONNIART, among others. But he says nothing more here of any relation between this petiole and the *Lyginodendron*-stem.

In 1887‡ WILLIAMSON returned to this question, and expressed his conviction that the petiole and stem belonged to the same plant; the conclusion "that *Lyginodendron Oldhamium* belongs to the group of Ferns" has, he says, "now made a near approach to certainty" (*loc. cit.*, p. 298); he extends the same view to *Heterangium*. A few lines further on he says, of these two genera, that "possibly they are the generalised ancestors of both Ferns and Cycads," citing *Stangeria* as a living plant retaining a similar combination of characters (*loc. cit.*, p. 299). In this passage WILLIAMSON clearly expresses the idea of an intermediate group, but with him the balance still inclined to the Fern side, for in 1890,§ after showing by identity of structural characters (the cortical emergences in particular) "that *Rachiopteris aspera* is merely a petiole of *Lyginodendron Oldhamium*," he adds: "it also follows that *L. Oldhamium* is a true Fern, most probably belonging to some Sphenopterid type" (*loc. cit.*, p. 91). In his General Index, too (1894), *Lyginodendron* is included under Filices.||

* *Loc. cit.*, p. 405.

† "Organisation, &c., Part VI.," 'Phil. Trans.,' B, vol. 164, Part II.

‡ *Loc. cit.*, Part XIII., 'Phil. Trans.,' B, vol. 178 (1887).

§ *Loc. cit.*, Part XVII., 'Phil. Trans.,' B, vol. 181 (1890).

|| WILLIAMSON, "General, Morphological, and Histological Index, &c.," 'Manchester Lit. and Phil. Soc. Mem. and Proc.,' 1893-4.

In the meantime FELIX, who found *Lyginodendron Oldhamium* in the Coal-measures of Westphalia, had suggested in 1885 a comparison with Cycads, and more especially with Medulloseæ, which were then classed with them.* In 1887, COUNT SOLMS-LAUBACH in his Introduction to Fossil Botany,† recognised with special reference to *Lyginodendron*, the existence of groups intermediate between Ferns and Gymnosperms. In subsequent memoirs he goes further, and strongly emphasises the significance of extinct types (*Lyginodendreae* among others), combining the characters of Filicineæ and Gymnosperms, and indicating the common origin of the two classes.‡

In the memoir on *Lyginodendron* and *Heterangium*, published in 1896 by Professor WILLIAMSON, in conjunction with one of the present writers,§ it was pointed out that the available evidence clearly indicated a position intermediate between Ferns and Cycads (*loc. cit.*, p. 704), and that the two genera are best regarded as the derivatives of an ancient and generalised Fern-stock, from which they already show a marked divergence in the Cycadean direction. In the absence of evidence as to the fructification the question whether it was more likely to have been Filicinean or Gymnospermous in character was regarded as perfectly open.

In 1897 POTONIÉ, in his textbook,|| established the class Cycadofilices for the group of Palæozoic plants, including *Lyginodendron*, already recognised as combining Cycad-like with Fern-like characters. His proposal has been generally adopted by subsequent writers on the subject.

In the same year ZEILLER¶ first called attention to the probability that the fructification of *Lyginodendron* was of the type of STUR's *Calymmatotheca Stangeri*; on the ground of this attribution ZEILLER inclined to the view that *Lyginodendron* was a true Fern, and was disposed to assign the same position to the other genera in question. In his 'Éléments de Paléobotanique' (1900), while recognising the group Cycadofilicinæ as distinct and without any direct analogue in the recent flora, he says that it would be rash to exclude them, on their vegetative characters alone, from the Ferns (*loc. cit.*, p. 125); as regards *Lyginodendron* in particular his opinion is that, judging from its probable *Calymmatotheca* fructification, it appears

* "Strukturzeigende Pflanzenreste a. d. oberen Steinkohlenformation Westphalens," 'Ber. d. Naturforsch. Gesellschaft z. Leipzig,' 1885, p. 7.

† English edition, pp. 141, 163, and 362.

‡ See, for example, his memoirs on *Protopitys Buchiana*, 'Bot. Zeitung,' 1893, p. 207, and on *Medullosa Leuckarti*, 'Bot. Zeitung,' 1897, p. 198.

§ WILLIAMSON and SCOTT, "Further Observations, &c., Part III.," 'Phil. Trans.,' B, vol. 186 (1895).

|| 'Lehrbuch der Pflanzenpalæontologie, &c.,' 2, Lieferung, 1897, p. 160. POTONIÉ has changed the name *Lyginodendron* to *Lyginopteris*, on the ground that the former genus was originally founded by GOURLIE on Lepidodendroid casts. This alteration has been adopted by some other palæobotanists; for reasons of convenience we have preferred to retain WILLIAMSON's nomenclature.

¶ "Sur quelques Fougères des Dépôts houillers d'Asie Mineure," 'Soc. Bot. de France Bull.,' vol. 44 (1897) p. 199.

to have been a true Fern.* Up to that time no one had expressed a doubt that *Calymmatotheca*, the only fructification which then appeared referable to *Lyginodendron*, was Filicinean. Hence, in 1900, one of the present writers, in a general survey of the Cycadofilices,† based the intermediate position of *Lyginodendron* and its allies wholly on evidence drawn from the structural characters of the vegetative organs, pointing out "that if we were to rely on reproductive characters alone, we should probably, on the existing evidence, agree with M. ZEILLER in regarding *Lyginodendron* as still belonging to the Filicales."‡

The position, then, previous to the present investigation was this: the evidence for the existence in Palæozoic times of an extensive group of plants transitional between Ferns and Cycads appeared overwhelmingly strong, and was regarded by certain botanists, including the present writers, as justifying the conclusion that the Cycadales, and not improbably the Gymnosperms generally, were derived from a Filicinean ancestry.§ This conclusion then depended entirely on a detailed comparative study of the vegetative, and especially of the anatomical characters. The evidence as to the reproductive organs of the Cycadofilices was extremely scanty: in *Lyginodendron*, where alone any significant data were available, there was a presumption that the fructification was of a type (*Calymmatotheca*) then generally accepted as Filicinean.

The results of the present investigation have placed the whole question in a new light. If our evidence be accepted—and short of the proof of the continuity it could scarcely be stronger—it follows that *Lyginodendron*, so far as the female fructification is concerned, had definitely crossed the boundary between Cryptogams and Spermophytes; as regards its seeds it was as true a Gymnosperm as any known Palæozoic plant. The morphology of the seed is discussed in another section (p. 230); here we need only say that though some features in its organisation may fairly be interpreted as primitive, the seed nature is as little open to doubt as in any Spermophyte of Palæozoic age. Thus the centre of gravity of the group (for, as is already clear, other Cycadofilices will prove to be likewise involved) has undergone a marked displacement in the Gymnospermous direction. Those who view intermediate groups with suspicion will now have to class *Lyginodendron* not as a true Fern, but as a true Gymnosperm, and that, indeed, would be its correct position if we were justified in simply applying the scheme of recent taxonomy to Palæozoic plants. *Lyginodendron* conforms, as nearly as any known contemporary plant, to the characters on which the division Gymnospermeæ is based. Yet the features on which an intermediate position between Ferns and Cycads was originally assigned to the

* *Loc. cit.*, p. 129. See also the author's discussion of the whole question, pp. 369–371.

† SCOTT, 'Studies in Fossil Botany,' 1900, Lectures X. and XI. Here the anatomical evidence is fully stated, and references will be found to the original memoirs dealing with the various plants in question.

‡ *Loc. cit.*, p. 336.

§ SCOTT, *loc. cit.*, pp. 514–522.

genus, retain all their former significance. In the whole of the foliar characters, whether structural or external, in the primary structure of both stem and root, and in the relation between the stem and the roots, *Lyginodendron* shows unmistakable affinity with the Ferns, and certainly stands incomparably nearer the Cryptogams of that class than does any plant included among recent Gymnosperms.

The question as to the nature of the male fructification still remains open. STUR's reference of his *Calymmatotheca Stangeri* to a *Sphenopteris*, almost identical with the foliage of *Lyginodendron Oldhamium*, is probably correct, but it is by no means certain that the *Calymmatotheca* in question represents a microsporangiate fructification. An examination of the original specimens, kindly lent for that purpose by the Director of the Geol. Reichsanstalt at Vienna to the Geological Department of the British Museum, leads us to accept STUR's interpretation of the tufted bodies terminating the pinnules as valves of a foliaceous "indusium," rather than to regard them with M. ZEILLER as of a sporangial nature.* Whether the cupule-like indusium enclosed a seed or a microsporangial sorus has not yet been determined; the actual reproductive organs, whatever they may have been, appear to have been shed previous to fossilisation.

Miss BENSON has discovered a fructification, with structure preserved, which she places in a new genus, *Telangium*, and is inclined to regard as the pollen-bearing synangium of *Lyginodendron Oldhamium*, with which the specimens occur in association.† If this attribution should prove to be correct, it would follow that the microsporangia of *Lyginodendron* had much in common with the fructification of undoubted Ferns, and the evidence for the Filicinean affinities of the genus would thus be further strengthened. For the present, however, it is safest to leave the microsporangia out of account, as this question is still involved in so much doubt.

On the whole of the evidence actually before us, the position of *Lyginodendron* as a member of a group of plants, transitional between Filicales and Gymnosperms, appears to be definitely established. While many of the Filicinean characters are retained, the plant, in the organisation of its seed, had fully attained the level of a Palaeozoic Gymnosperm.

The absence of any indication of an embryo within the ripe seed is a negative character which our plant shares with all the known Spermophytes of its period. Strictly speaking we have no proof that any of these plants possessed seeds corresponding to the current definition, in which the presence of an embryo forms an essential character.‡ On this ground it might appear desirable to establish a group

* The statement of this question given on a former occasion by one of us (SCOTT, 'Studies in Fossil Botany,' p. 325) now requires modification in the sense indicated above.

† "The Fructification of *Lyginodendron Oldhamium*," 'Annals of Botany,' vol. 16, 1902. Full paper since published, 'Ann. of Bot.,' vol. 18, p. 161, 1904.

‡ See above, p. 231; also SCOTT, "Origin of Seed-bearing Plants," lecture delivered before the Royal Institution, May 15, 1903, p. 6.

analogous to, though by no means co-extensive with the Progymnosperms of SAPORTA and MARION,* for the Palæozoic Spermophytes. Such a group would embrace all the plants of that period of which the seeds are known, including the Cordaiteæ. The latter, however, approach much nearer to the Gymnosperms than is the case with *Lyginodendron*, as shown by their whole vegetative organisation, by their complex inflorescence, and generally, by their wide divergence from the Fern type, from which they appear far more remote, even than recent Cycads. For these reasons we do not propose to disturb the Cordaiteæ in the place among Gymnosperms which has been generally accorded them. To do so would involve a re-consideration of the position of the recent Cycadaceæ and of *Ginkgo* in which fertilisation also takes place at a late stage, while the degree of development of the embryo within the ripe seed appears to be very variable. It is, however, desirable that some group, more definite than the Cycadofilices, should be formed for those Palæozoic plants, of Filicinean affinities, which prove to have possessed seeds. Mr. KIDSTON's discovery of the seed of *Neuropteris heterophylla*, already referred to (p. 230) indicates that such a group will soon be well furnished with members. There is abundant evidence that the *Neuropteris* fronds were the foliage of some of the Medulloseæ; there is thus every reason to anticipate that the whole of this family, so well characterised anatomically and morphologically, will prove to have been seed bearing; there is already some direct evidence for the attribution of the seed *Trigonocarpon olivaforme* to a *Medullosa*,† and these indications are much strengthened by the analogy of Mr. KIDSTON's *Neuropteris*. Thus it appears that the Medulloseæ as well as the Lyginodendreæ are rapidly qualifying for a place among primitive Spermophyta.

The present group or association Cycadofilices was founded expressly on vegetative and anatomical characters,‡ it has served its purpose in emphasising the existence of a great plexus of Palæozoic plants combining Filicinean with Gymnospermous features. Now, however, we are in a position to advance further, for we know that some at least of these transitional types, while retaining much of the Filicinean organisation, had already entered the ranks of seed-bearing plants. It appears to us that the presence in the Palæozoic flora of these primitive, Fern-like Spermophytes, so important as a phase in the history of evolution, may best be recognised by the foundation of a distinct class which may suitably be named *Pteridospermeæ*. The proposed class may be provisionally defined as embracing those Palæozoic plants with the habit and much of the internal organisation of Ferns, which were reproduced by means of seeds. A more exact definition must await more extended knowledge of the reproductive characters; it is, however, not improbable that the radial symmetry of the seed, and the occurrence of fertilisation at a late stage, when the ovule had already acquired the mature structure of a ripe seed, as well as the postponement

* 'L'Évolution du Règne Végétal.—Les Phanérogames,' vol. 1, pp. 17, 62, and 68.

† G. WILD, "On *Trigonocarpon olivaforme*," 'Manchester Geol. Soc. Trans.,' vol. 26, 1900

‡ See POTONIÉ, 'Lehrbuch,' p. 160.

of embryonic development, may prove to have characterised these early seed plants.

We shall probably incur little risk of error if we already place the Lyginodendreae and Medulloseae in the new class Pteridospermeae. The group Cycadofilices will continue to be employed for those transitional families, where we have as yet no evidence to show how far the reproductive advance had proceeded. Such a family for example, as the Cladoxyleae, must remain for the present in a wholly undetermined position, for we have no indications here to show whether anatomical progress had or had not been accompanied by any marked advance on Cryptogamic methods of reproduction.

The further development of our knowledge of the Pteridosperms will form one of the chief objects of palaeo-botanic investigation in the near future.

In conclusion the authors desire to express their thanks to Mr. J. LOMAX, whose skill and good judgment in the collection and preparation of the material have been of essential service; all the sections of the seed which WILLIAMSON appropriately named in his honour, are from his hand. They are further greatly indebted to Miss M. C. STOPES, for her invaluable assistance, at a critical stage of the investigation, in obtaining evidence by searching the WILLIAMSON and other extensive collections, and to Mr. L. A. BOODLE who, in addition to contributing a large part of the illustrations, has been in close touch with the investigation throughout.

EXPLANATION OF PLATES 4-10.

Plates 4-6.—Photographs from the sections. In most cases they should be examined with the aid of a hand-lens. Photographs 1-7 and 14-27 are by Mr. L. A. BOODLE. Photographs 8-13 by Mr. W. TAMS, of Cambridge.

PLATE 4.

Phot. 1.—Longitudinal section of a small arrested seed enclosed in its cupule, which loosely invests it on all sides. The cupule bears numerous glands with hollow heads. In the seed the testa, chalaza, canopy, pollen-chamber, and other parts are seen, as shown more in detail in photos. 2 and 3.

W. 1931, A. \times about 15. (See pp. 211 and 216.)

Phot. 2.—Upper part of the same seed. *t.*, testa, consisting of young palisade layer and hypoderm: *l.*, a loculus of the canopy; *s.*, sinus, or space between inner wall of canopy and wall of pollen-chamber; *p. c.*, the bell-shaped pollen-chamber surrounding the central cone, which is not quite in median section; *p. c.'*, tube of chamber, projecting beyond the micropyle.

W. 1931, A. \times about 36. (See p. 200.)

Phot. 3.—Lower part of the same seed, slightly overlapping the part shown in phot. 2. *a. l.*, abscission-layer; *ch. c.*, the bulky chalazal cushion, displaced upwards, as seen in phot. 1; *v. b.*, vascular bundle of chalaza, branching out above into bundles which traverse the contracted intermediate sac, *i. s.*; *mg.*, membrane of megaspore, which is seen complete, but contracted.

W. 1931, A. \times about 45. (See p. 212.)

Phot. 4.—Another small cupulate seed, in tangential section. *c.*, cupule, bearing many glands; *gl.*, the gland represented in phot. 22. Above the seed the cupule encloses a pinnule of *Lyginodendron*, *Ly.*; *a. l.*, abscission-layer; *ch.*, chalaza; *t.*, testa, with conspicuous hypoderm; *s.*, sinus; *w.*, wall of pollen-chamber in tangential section; *m.*, micropyle. In the body of the seed three vascular bundles are seen.

W. 1931. \times about 20. (See pp. 211, 212.)

Phot. 5.—Full-sized seed in longitudinal section. At the chalaza the section is fairly median, but at the micropylar end it misses the central cone of the pollen-chamber. Otherwise all the parts of the seed are shown, as represented in detail in photos. 6 and 7. *mg.*, contracted membrane of megaspore.

W. 1930. \times about 10. (See p. 198.)

Phot. 6.—Upper part of the same seed. *pal.*, palisade layer of testa; *o. t.*, outer, *i. t.*, inner wall of canopy, the loculus between them contains some remains of tissue; *s.*, sinus; *w.*, wall of pollen-chamber, projecting slightly beyond micropyle at *p. c.*; *mg.*, membrane of megaspore, within which remains of prothallial tissue are seen.

W. 1930. \times about 26. (See p. 200.)

Phot. 7.—Lower part of the same seed. *a. l.*, abscission-layer; *ch. c.*, chalazal cushion; *v. b.*, vascular bundle of chalaza (*cf.* Plate 7, fig. 5); *i. s.*, intermediate sack; *mg.*, membrane of megaspore contracted.

W. 1930. \times about 26. (See p. 207.)

PLATE 5.

Phot. 8.—Slightly oblique longitudinal section of a full-sized seed. The pollen-chamber (*p. c.*) is cut in a tangential plane and shows two groups of pollen-grains (*p. g.*). *c. c.*, central cone of pollen-chamber; *o.*, orifice of pollen-chamber; *s.*, sinus round the pollen-chamber; *l.*, loculus of canopy; *t.*, testa. The lower end of the section falls outside the abscission-layer. The pollen-chamber of this specimen is enlarged in Plate 9, fig. 21.

U. C. L., R. 2. \times about 16. (See p. 200.)

Phot. 9.—Longitudinal section of a full-sized seed. The section falls outside the pollen-chamber at the apex, but approaches the axis of the seed in its lower part. *se.*, *se'*, complete and incomplete septa of canopy; *l.*, loculus of canopy; *pl.*, plinth or mound upon the summit of which the pollen-chamber stands; *i. s.*, intermediate sack contracted; *v. b.*, *v. b.*, vascular bundles; *mg.*, contracted membrane of megaspore containing prothallial tissue; *nu.*, tissue at base of nucellus.

U. C. L., R. 3, *a.* \times about 13. (See p. 203.)

Phot. 10.—Very oblique section across the top of a full-sized seed, cutting two of the loculi of the canopy tangentially in the plane of the vascular bundles. *p. c. w.*, wall of pollen-chamber; *c. c.*, central cone of pollen-chamber; *l.*, *l.*, loculi of canopy cut in tangential section; *v. b.*, *v. b.*, vascular bundles of these loculi, abutting below on the bundle-ring; *se.*, *se.* septa separating the loculi; *pal.*, *hy.*, palisade and hypodermal layers of testa; *rid.*, ridge around the micropyle, cut obliquely.

U. C. L., R. 9, *c.* \times about 40. (See p. 204.)

Phot. 11.—Testa from specimen in phot. 9 (right hand, at base), more highly magnified, and rotated through 90°. *pal.*, palisade-layer bearing pegs (*pe.*, *pe.*) with normal preservation; *hy.*, hypoderm of testa; *nu.*, tissue at base of mucellus; *ch. c.*, chalazal cushion.

U. C. L., R. 3, *a.* × about 46. (See p. 206.)

Phot. 12.—Transverse section of testa of full-sized seed, with palisade cells and mucilage cones. *pal.*, palisade cells; *mu.*, mucilage cones; *pe.*, position of peg raised on a mucilage cone; *hy.*, hypoderm of testa.

U. C. L., R. 8, *b.* × about 100. (See p. 206.)

Phot. 13.—Approximately transverse section of the chalaza of a full-sized seed with chalazal vascular bundle (testa shown on *lower* side of photograph only). *v. b.*, vascular bundle; *ch. c.*, chalazal cushion; *pal.*, palisade-layer of testa.

U. C. L., R. 8, *a.* × about 45. (See p. 208.)

Phot. 14.—Transverse section of one of the vascular bundles of the seed (that marked *v. b.* in Plate 7, fig. 2). *i. s.*, part of the "intermediate sack" on which the bundle abuts; *mg.*, part of the megasporangium membrane. In the bundle only the xylem is evident; the smaller elements are on the whole directed towards the inner side.

W. 1915, O. × about 200. (See p. 210.)

Phot. 15.—Longitudinal section of cupulate seed and pedicel. The section is obliquely tangential, approaching the median plane at the lower end. *p.*, pedicel on which the seed is borne; *c. c.*, cupule, bearing glands; on each side it extends a little above the reference-line; *t.*, testa of seed; *ch. c.*, chalazal cushion. Cf. Plate 10, fig. 33. Portions of the seed are shown enlarged in photos. 16 and 21.

S. 558. × 13. (See p. 217.)

PLATE 6.

Phot. 16.—Chalazal portion of the seed shown in phot. 15. *c.*, cupule, showing a vascular bundle and bearing several glands; that marked *gl.* is shown on a larger scale in phot. 21; *ch. c.*, chalazal cushion; *pal.*, palisade-layer; *hy.*, hypoderm of testa.

S. 558. × about 35. (See p. 217.)

Phot. 17.—Detached cupule, seen in approximately tangential section; the base of the cupule is towards the left; several glands are shown; that marked *gl.* is represented further enlarged in phot. 23. The course of the bundles traversing the cupule is shown in the semi-diagrammatic fig. 11, Plate 8.

U. C. L., R. 14, *a.* × 28. (See p. 219.)

Phot. 18.—Transverse section of a small petiole of *Lyginodendron Oldhamium*, showing the characteristic vascular bundle and hypoderm. Numerous glands are present, in three of which the head is seen to be hollow; cf. phot. 19.

S. 625. × 15. (See p. 227.)

Phot. 19.—Portion of the same petiole enlarged, showing the three glands with the head in the hollow state of preservation. *hy.*, hypoderm, with radial sclerotic bands.

S. 625. × 36. (See p. 227.)

Phot. 20.—Gland from another section of the same petiole, for comparison with the gland shown in phot. 21 from the cupule of *Lagenostoma Lomaxi*. The head of the gland is completely empty, while the tissue of the stalk is well preserved. *hy.*, sclerotic band of hypoderm.

U. C. L., M. 11, *c.* \times 70. (See p. 227.)

Phot. 21.—Gland (marked *gl.* in phot. 16) from the cupule of *Lagenostoma Lomaxi*, for comparison with the petiolar gland shown in phot. 20. *v. b.*, a vascular bundle of the cupule.

S. 558. \times 70. (See pp. 223 and 227.)

Phot. 22.—Gland (marked *gl.* in phot. 4) on the cupule of a small seed. Note the pear-shaped cavity of the head. *c.*, cupule; *pal.*, palisade-layer; and *hy.*, hypoderm of the testa of the seed.

W. 1931. \times 54. (See p. 224.)

Phot. 23.—Gland (marked *gl.* in phot. 17) from a cupule. *gl. t.*, remains of glandular tissue in the cavity of the head. Below, a part of the vascular bundle *d.* (see Plate 8, fig. 11) is seen. *sh.*, *sh.*, large-celled bundle-sheath.

U. C. L., R. 14, *a.* \times about 60. (See p. 223.)

Phot. 24.—Detached vegetative gland, to show the typical structure. Compare Plate 8, fig. 18, where a similar though longer gland is shown *in situ* on the stem. *gl. t.*, glandular tissue of the head, almost perfectly preserved. The structure of the stalk is also well shown. *st.*, depressed stoma.

S. 447. \times about 60. (See p. 226.)

Phot. 25.—Detached vegetative gland. The glandular tissue, *gl. t.*, has here become somewhat dis-organised.

W. 1931, A. \times about 80. (See p. 227.)

Phot. 26.—Detached vegetative gland. Here the glandular tissue, *gl. t.*, is breaking down, showing a lenticular gap in the middle.

W. 1931, A. \times about 80. (See p. 227.)

Phot. 27.—Vascular bundle, in transverse section, from a small rachis of *Lyginodendron Oldhamium*, to compare with the bundle from the pedicel of the seed shown in Plate 8, fig. 10. Only the xylem is preserved; *px.*, position of median protoxylem group. Lateral protoxylem was no doubt present also, to the right and left.

S. 448. \times about 80. (See pp. 221 and 228.)

PLATES 7-10.

Figures from camera lucida drawings. Those in Plates 7 and 8 by Mr. L. A. BOODLE; Plate 10, figs. 27, 28, 28A and B, and 34 by Miss M. C. STOPES; all the other figures by one of the authors.

PLATE 7.

Figs. 1-3.—Series of three approximately transverse sections of the same seed; the orientation of the sections is uniform throughout the series.

Fig. 1.—Uppermost section, passing through the canopy. *c.*, *c.*, portions of the cupule, containing vascular bundles and bearing glands; *pal.*, palisade; *hy.*, hypoderm of testa, cut obliquely; *l.*, *l.*, loculi of the canopy (nine in all), separated by radial septa; *i. t.*, inner wall of canopy; *p. c. w.*, wall of pollen-chamber; *c. c.*, central cone of pollen-chamber.

W. 1915, M. \times 18 $\frac{1}{2}$. (See pp. 198, 204, and 218.)

Fig. 2.—Middle section through the body of the seed. *c.*, *c'*, portions of the cupule, of which many fragments are shown; *c'*, the largest continuous piece (a number of glands and vascular bundles are shown); *v. b.*, the bundle represented in fig. 16; *pal.*, palisade; *hy.*, hypoderm of testa; *i. s.*, intermediate sack on which the nine vascular bundles abut; *v. b'*, the bundle represented in Plate 5, phot. 14; *mg.*, membrane of megasporangium.

W. 1915, O. $\times 18\frac{1}{2}$. (See pp. 198 and 218.)

Fig. 3.—Lowest section, through chalaza. *c.*, *c'*, cupule, which is here nearly complete; *pal.*, *hy.*, palisade and hypoderm of testa, cut obliquely; *ch. c.*, chalazal cushion; *v. b.*, vascular bundle of chalaza, shown enlarged in fig. 4.

S. 236. $\times 18\frac{1}{2}$. (See pp. 198 and 218.)

Fig. 4.—Vascular bundle of chalaza and surrounding tissues, transverse section. In the xylem the smallest elements are nearly central (*cf.* fig. 5). The phloëm is not well defined.

S. 236. $\times 90$. (See pp. 209 and 210.)

Fig. 5.—Vascular bundle and surrounding tissues of chalaza in longitudinal section. *px.*, central protoxylem of bundle; *nu.*, tissue at base of nucellus; *ch. c.*, part of the chalazal cushion (*cf.* Plate 4, phot. 7).

W. 1930. $\times 98$. (See pp. 209 and 210.)

Fig. 6.—Part of a vascular bundle from a full-grown seed, in approximately radial section. *i.*, inner; *o.*, outer side; *px.*, protoxylem element. The other tracheides are spiral or scalariform, and in one case pitted. Some of the narrow elements adjacent to the xylem may be phloëm.

W. 1931, A. $\times 390$. (See p. 210.)

Fig. 7.—Transverse section through the lower part of a cupule, bearing numerous glands and containing vascular bundles. *c.*, *c'*, cupule; *b. s.*, *b. s.*, tissue at base of seed; *h.*, hair represented in fig. 8. The specimen is split into two unequal parts by a wide crack.

Section lent by Miss BENSON. H. 55. $\times 18\frac{1}{2}$. (See p. 217.)

PLATE 8.

Fig. 8.—Hair, from the cupule shown in fig. 7.

H. 55. $\times 390$. (See p. 224.)

Fig. 9.—Cupule and pedicel in approximately tangential section. *p.*, pedicel; *c.*, *c'*, cupule, one portion of which is detached; *gl.*, gland *in situ*; *b. s.*, tissue at base of seed, which is lost; *v. b.*, vascular bundle of pedicel, represented enlarged in fig. 10; *v. b'*, bundles passing out into cupule.

U. C. L., R. 15. $\times 18$. (See p. 220.)

Fig. 10.—Vascular bundle of pedicel shown in fig. 9, in somewhat oblique transverse section. Some of the gaps in the wood probably represent position of protoxylem.

U. C. L., R. 15. $\times 175$. (See p. 220.)

Fig. 11.—Cupule, in approximately tangential section, shown also in Plate 6, phot. 17. *a*, vascular bundle of pedicel; *b*, *c*, *d*, *e*, *f*, *g*, *h*, *i*, vascular bundles of cupule; *gl.*, *gl.*, glands.

U. C. L., R. 14, *a*. $\times 18$. (See p. 219.)

Fig. 12.—Part of the vascular bundle marked *e* in fig. 11, showing xylem with phloëm on each side. *px.*, protoxylem; *ph.*, *ph.*, phloëm; *sh.*, *sh.*, bundle-sheath.

U. C. L., R. 14, *a*. $\times 150$. (See p. 222.)

Fig. 13.—Part of the vascular bundle marked *b.* in fig. 11, showing a large tracheide with multiseriate bordered pits.

U. C. L., R. 14, *a.* $\times 390$. (See p. 222.)

Fig. 14.—Detached portion of cupule, bearing glands. Two vascular bundles are shown; that marked *v. b.* is represented in fig. 15. The arrow has the same direction as in that figure.

U. C. L., R. 14, *a.* $\times 18\frac{1}{2}$. (See p. 222.)

Fig. 15.—The vascular bundle marked *v. b.* in fig. 14. *x.*, the large-celled xylem; *ph.*, phloem; *sh.*, bundle-sheath. The arrow, as in fig. 14, points outwards, showing that the orientation of the bundle is, in this case, reversed.

U. C. L., R. 14, *a.* $\times 390$. (See p. 222.)

Fig. 16.—Another vascular bundle from a cupule (that marked *v. b.* in fig. 2). *px.*, protoxylem, in the interior of the xylem strand; *ph.*, phloem. The arrow points outwards (parallel to the axis of the adjacent gland, see fig. 2), and thus the orientation is here normal.

W. 1915, O. $\times 390$. (See p. 222.)

Fig. 17.—Long gland borne on a cupule. *c.*, cupular tissue; *gl. t.*, remains of glandular tissue in cavity of head.

U. C. L., R. 14, *b.* $\times 38$. (See p. 223.)

Fig. 18.—Long gland, borne on a stem of *Lyginodendron Oldhamium*. *co.*, cortex of stem; *gl. t.*, glandular tissue of the head, perfectly preserved. The peripheral wall of the head is broken at the top.

S. 1781. $\times 38$. (See p. 225.)

PLATE 9.

Figs. 19–25, *Lagenostoma Lomaxi*.

Fig. 19.—Nearly median longitudinal section of the pollen-chamber and adjacent parts of a full-sized seed. *p. c.*, cavity of pollen-chamber; *p. g.*, pollen-grain (two are present); *c., c.*, central cone of pollen-chamber; *o.*, orifice of pollen-chamber; *s.*, sinus between canopy and pollen-chamber; *pl.*, plinth supporting the pollen-chamber; *i. t.*, inner wall of canopy or integument; *o. t.*, outer wall of canopy; *r.*, ridge on testa radiating from micropyle. The ridge is cut obliquely, owing to the section being slightly tangential and oblique; *mg.*, crumpled wall of megasporangium.

U. C. L., R. 1. $\times 60$. (See p. 200.)

Fig. 20.—Oblique section of a full-sized seed. The section starts near the micropyle, cutting the two middle loculi of the canopy as it enters almost transversally. It then strikes the pollen-chamber at mid-height, and, sloping down, cuts its base almost at the full diameter; continuing, the section cuts the intermediate sack and megasporangium obliquely and travels out of the seed about two-thirds down the side remote from that at which it entered. *l.*, loculus of canopy; *s.*, septum of canopy (still showing the compressed groove in its median plane); *r.*, ridges on surface overlying the septa of the canopy; *p. c.*, pollen-chamber; *p. g.*, pollen-grain; *c., c.*, central cone of pollen-chamber; *s.*, sinus around plinth and pollen-chamber; *v. b., v. b.*, vascular bundles abutting on the intermediate sack (*i. s.*); *mg.*, megasporangium.

Section lent by Professor F. E. WEISS. Manchester Collection, K₂, 14257. $\times 27$. (See p. 200.)

Fig. 21.—A somewhat tangential section of a pollen-chamber of a full-sized seed. *p. c. w.*, wall of pollen-chamber. Below, in the middle of the figure, just where the pollen-chamber is constricted, a portion of the wall is cut tangentially. *p. g., p. g.*, pollen-grains lying in the cavity of the pollen-chamber (about half a dozen are present); *c., c.*, central cone of tissue; *o.*, orifice of pollen-chamber; *r.*, ridge on outside of canopy, cut obliquely; *i. t.*, inner wall of canopy; *s.*, sinus round pollen-chamber; *pl.*, plinth.

U. C. L., R. 2. \times 62. (See p. 200.)

Fig. 22.—Oblique section across the canopy and pollen-chamber of a full-sized seed. The section entered the seed at the very edge of the micropyle, where it cuts three of the ridges (*r. r.*) obliquely. It passes obliquely into the neck of the pollen-chamber (*p. c.*), in leaving which it follows the plane of the wall (*p. c. w.*) for some distance. Below and flanking the pollen-chamber is the gap or sinus (*s.*). Two loculi of the canopy (*l. l.*) are cut into on either side, and the lower pair of loculi show their vascular strands (*v. b., v. b.*) lying in the plane of section. Part of the inner tangential wall of a fifth loculus is seen as an island of tissue (*i. t.*); *se., se.*, septa separating loculi. The transverse bar below these structures is the bundle-ring (*b. r.*). It is continued up on the left side as far as the second septum. The section passes out of the seed a little more than one-third of way down.

KIDSTON Collection, 260. \times 20. (See p. 200.)

Fig. 23.—Transverse section across the canopy and pollen-chamber of a small-sized seed. *p. c. w.*, wall of pollen-chamber, shifted somewhat from its true position. On the left the cells are much displaced; *s.*, sinus; *i. t.*, inner, fluted face of canopy; *f.*, groove on inner face of canopy; *l., l.*, loculi of canopy; *se., se.*, septa—both those shown are double; *v. b.*, vascular bundle lying in a loculus; *o. t.*, outer wall of canopy.

U. C. L. Collection, R. 11. \times 95. (See p. 203.)

Fig. 24.—Median longitudinal section of a young abortive seed. The pollen-chamber (*p. c.*) stands in the centre of the figure with its central cone of tissue (*c., c.*) rising from the base. The tube of the pollen-chamber (*p. c'.*) projects from the micropyle. Separated from the wall by the sinus (*s.*) is the canopy. *i. t.*, inner wall; *o. t.*, outer wall of canopy; *r.*, ridge at the micropyle. The plinth was undeveloped at this stage of development.

W. 1931, A., small seed. \times 65. (See p. 200.)

Fig. 25.—An oblique section across the canopy of a full-sized seed. As in fig. 22, this section enters the seed close to the micropyle cutting across a pair of ridges (*r.*) very obliquely; it then (unlike fig. 22) slopes *away from* the pollen-chamber, cutting the middle loculus of the canopy (*l'.*) parallel to its inner wall. *l., l.*, other loculi of canopy; *a. and b.*, vascular bundle cut twice, once below the canopy (*a.*) and again as it runs up the loculus (*b.*); *b. r.*, bundle-ring; *s.*, sinus; *s. e.*, septum of canopy; *i. t.*, inner wall of canopy. The section leaves the seed about half-way down the same side as that which it entered.

KIDSTON Collection, 424. \times 21. (See p. 204.)

PLATE 10.

Figs. 26–34, *Lagenostoma Lomaxi*.

Fig. 26.—Slightly oblique longitudinal section of the chalaza of a full-sized seed. *a. l.*, marks the position of the abscission-layer; *ch. c.*, the chalazal cushion; *pal.*, the palisade layer, thinning out at the seed-base; *hy.*, the fibrous hypoderm; *v. b.*, three of the branch vascular strands shown, one in transverse, the other two in somewhat oblique section. The main chalazal bundle does not lie in the plane of section; *nu.*, tissue at base of nucellus.

U. C. L. Collection, R. 4. \times about 60. (See p. 207.)

Fig. 27.—Oblique section through the chalazal region of a full-sized seed. Starting rather near the periphery of the scar and passing upwards and inwards, the section strikes the axis of the seed just at the point of branching of the chalazal bundle. Here the bundle *a* is cut nearly transversely, *b* longitudinally, and *c* obliquely. Three bundles run entirely outside the plane of section, whilst the remaining three, *d*, *e*, and *f*, are cut higher in their course after they have turned the corner of the intermediate sack. *a. l.*, abscission-layer; *ch. c.*, fibres of the chalazal cushion, cut nearly transversely in the lower part of the figure; *nu.*, tissue at base of nucellus; *pal.*, palisade-layer.

Section lent by Professor C. E. BERTRAND, Lille, Lab. Bot. Collection, 1110. \times 43. (See p. 207.)

Figs. 28, 28A, and 28B.—Palisade cells with pegs from full-sized seed.

All from Lille, Bot. Lab. Collection, 1108.

Another section from the seed given in fig. 27.

\times about 180. (See p. 206.)

Fig. 28.—A palisade cell (*pal.*) with peg (*pe.*).

Fig. 28A.—Two palisade cells with pegs. This figure shows the most usual type of preservation.

Fig. 28B.—Several palisade cells with pegs raised to various heights by mucilage cones. *pal.*, palisade cells; *hy.*, hypoderm; *pe.*, pegs; *mu.*, mucilage-cone.

Fig. 29.—Portion of a transverse section of the wall of a full-sized seed from about the middle part of the seed showing a vascular bundle cut *in situ*. *pal.*, palisade-layer; *pe.*, peg; *hy.*, hypoderm, with "thick" preservation; *v. b.*, vascular bundle; *mg.*, megasporangium.

U. C. L. Collection, R. 7, b. \times about 100. (See p. 209.)

Fig. 30.—Portion of a transverse section of a full-sized seed cut at a height corresponding to the insertion of the pollen-chamber. *pal.*, palisade-layer; *o. s.*, outer sack of the seed; *b. r.*, bundle-ring; *v. b.*, vascular bundle; *i. t.*, internal wall of canopy.

U. C. L. Collection, R. 6, c. \times 32. (See p. 203.)

Fig. 31.—Portion of intermediate sack (*i. s.*) from a transverse section cut half-way up the same seed.

The bundles, *v. b.*, *v. b.*, are connected, as usual, by the bundle-ring (*b. r.*), from which at places an inner ring (*i. r.*) has separated; *mg.*, megasporangium wall. (*b. r. + i. r. = i. s.*)

U. C. L. Collection, R. 6, b. \times 60. (See p. 202.)

Fig. 32.—Papillæ from a ridge near the micropyle of a small seed.

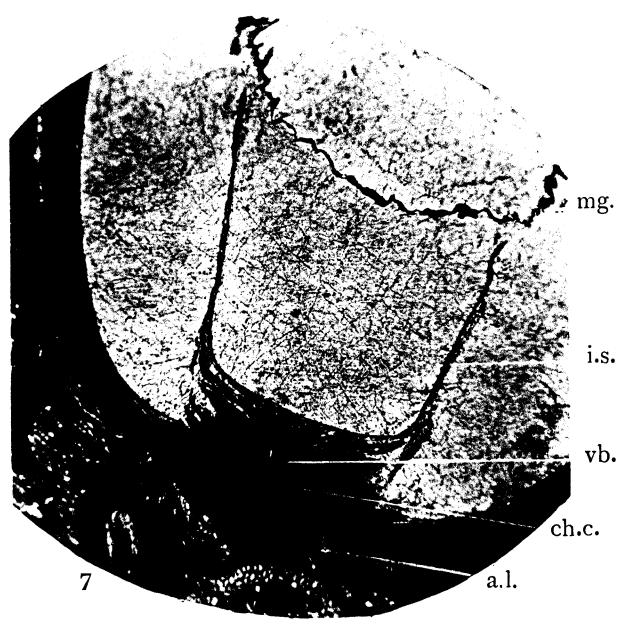
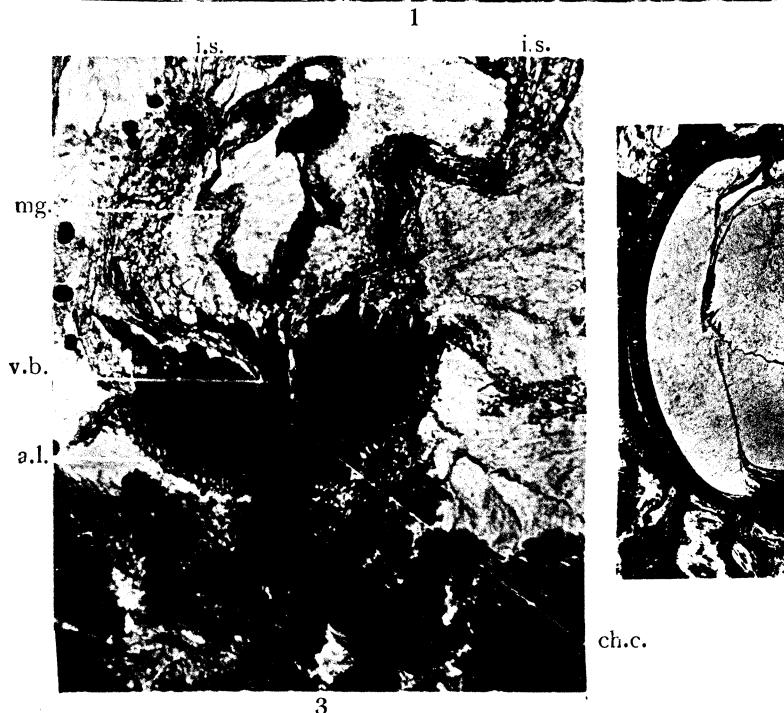
W. 1931, A. (small seed). \times about 400. (See p. 206.)

Fig. 33.—Longitudinal section through a full-sized seed showing continuity of seed-base with the pedicel and insertion of the cupule. *p.*, pedicel; *v. b.*, vascular bundle of pedicel; *c.*, *c.*, cupule; *gl.*, *gl.*, glands on pedicel and cupule; *a. l.*, abscission-layer; *ch. c.*, chalazal cushion; *pal.*, palisade-layer. See also photos. 15 and 16.

S. 558. \times about 15. (See p. 217.)

Fig. 34.—Median longitudinal section of a young seed or ovule, showing continuity of seed, pedicel, and cupule. The irregular black, knob-like layer is the surface of the testa, curiously preserved. The black pipes in the interior of the seed represent sections of the collapsed and folded megasporangium and nucellus. *p.*, pedicel; *c.*, *c.*, cupule; *c'*, long lobe of cupule; *gl.*, *gl.*, glands; *h.*, tuft of uniseriate hairs on long lobe of cupule; *ch.*, chalaza, somewhat above position of abscission-layer; *pal.*, young palisade-layer; *i. s.*, collapsed megasporangium and nucellus; *p. c. w.*, pollen-chamber wall; *c.*, *c.*, central cone of pollen-chamber; *o.*, orifice of pollen-chamber; *s.*, sinus; *v. b.*, *v. b.*, vascular bundles; *a.*, point of insertion of bundle to cupule.

U. C. L. Collection, R. 13. \times about 33. (See p. 213.)

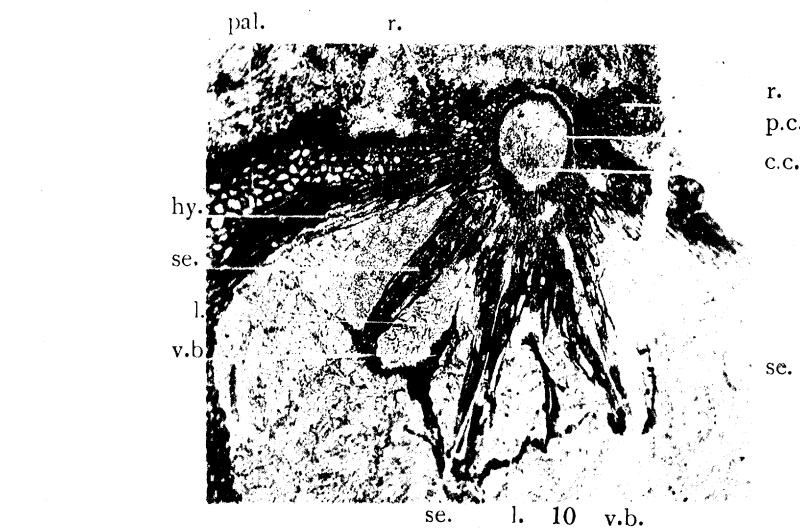




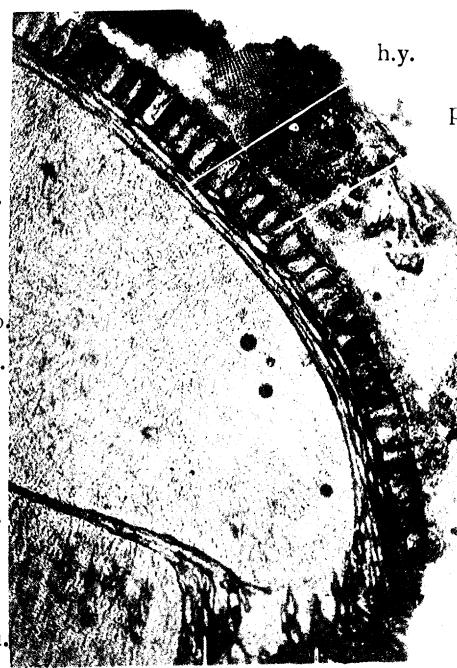
8



9 t



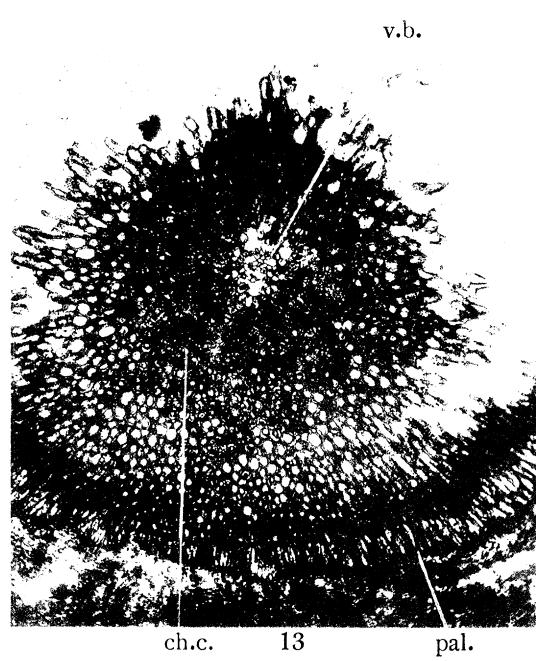
se. l. 10 v.b.



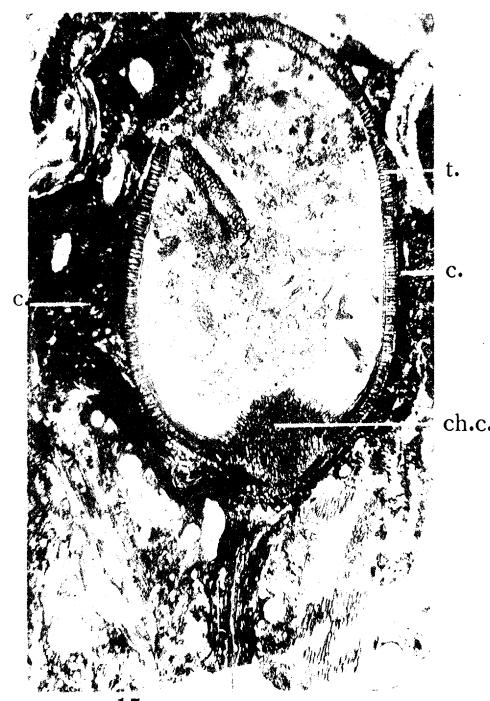
11 nu. ch .c.



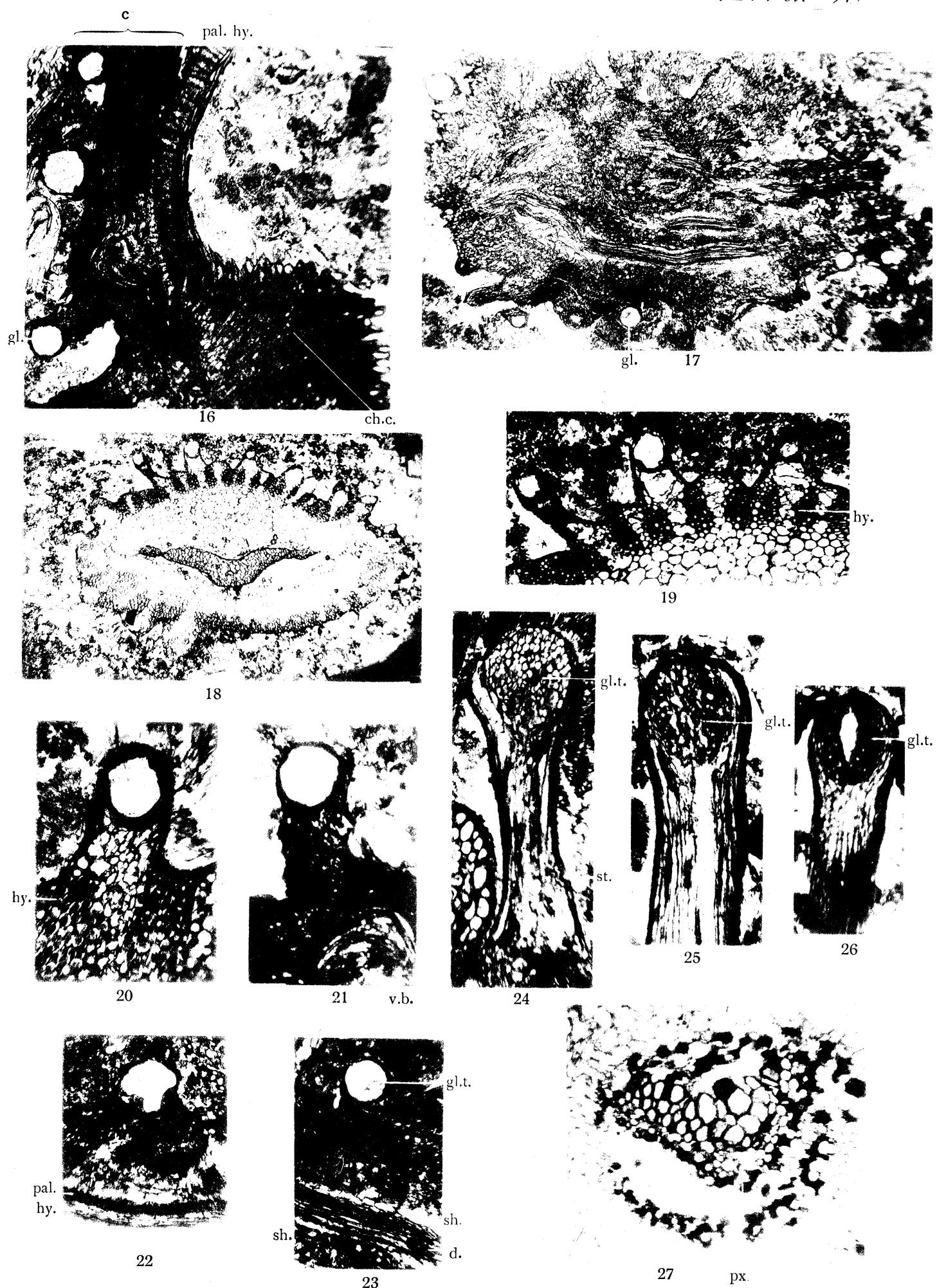
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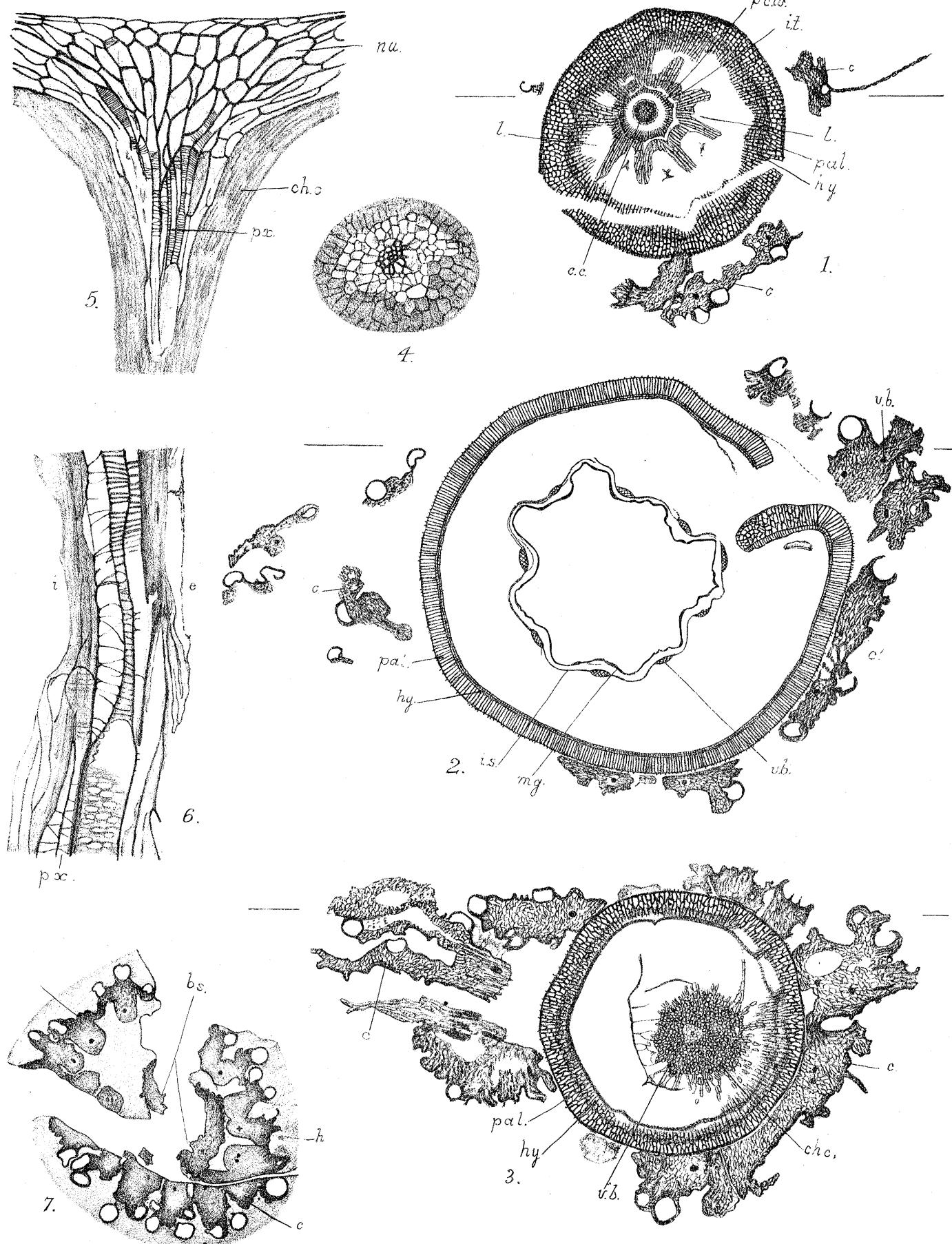


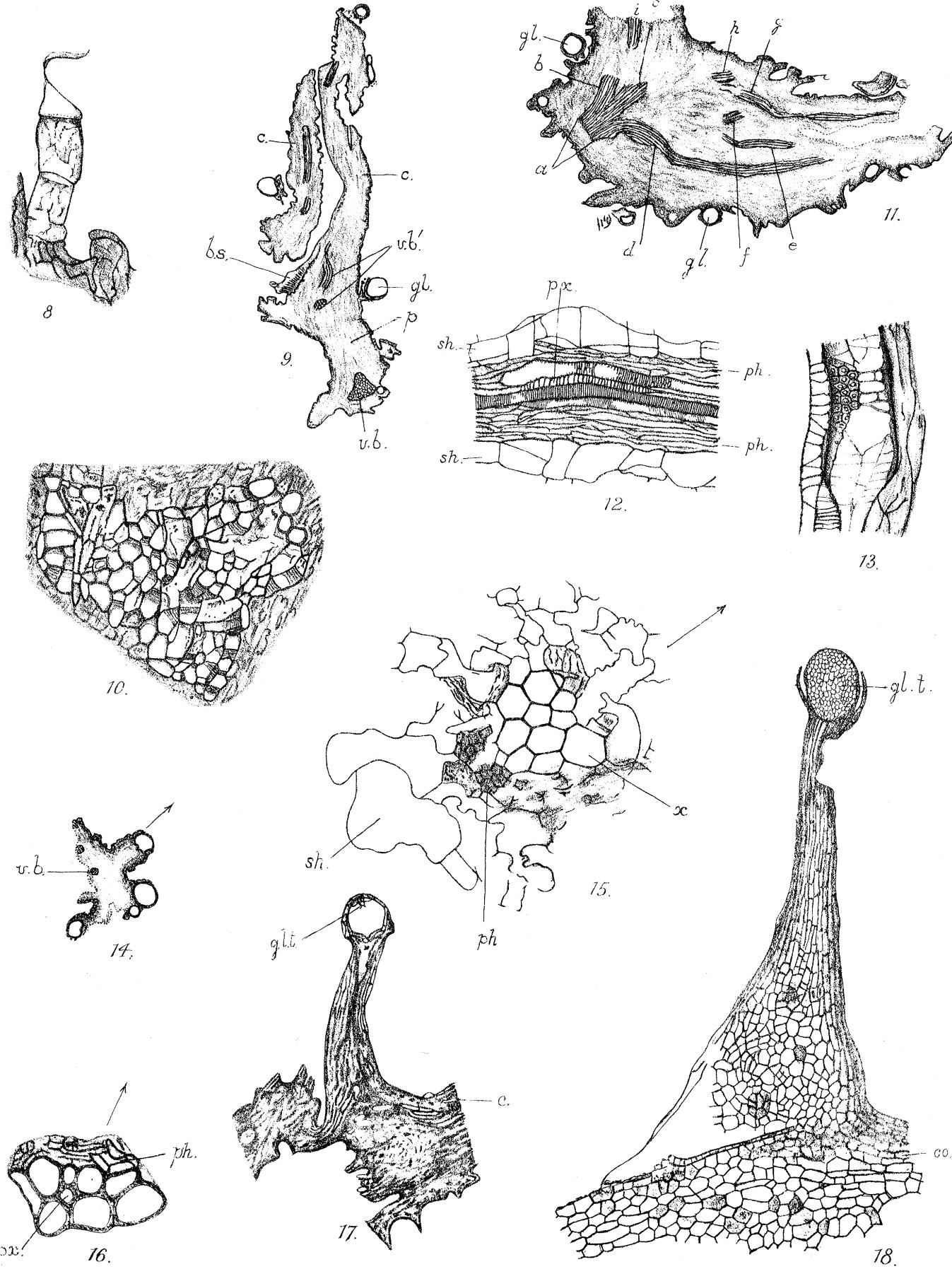
ch.c. 13 pal.

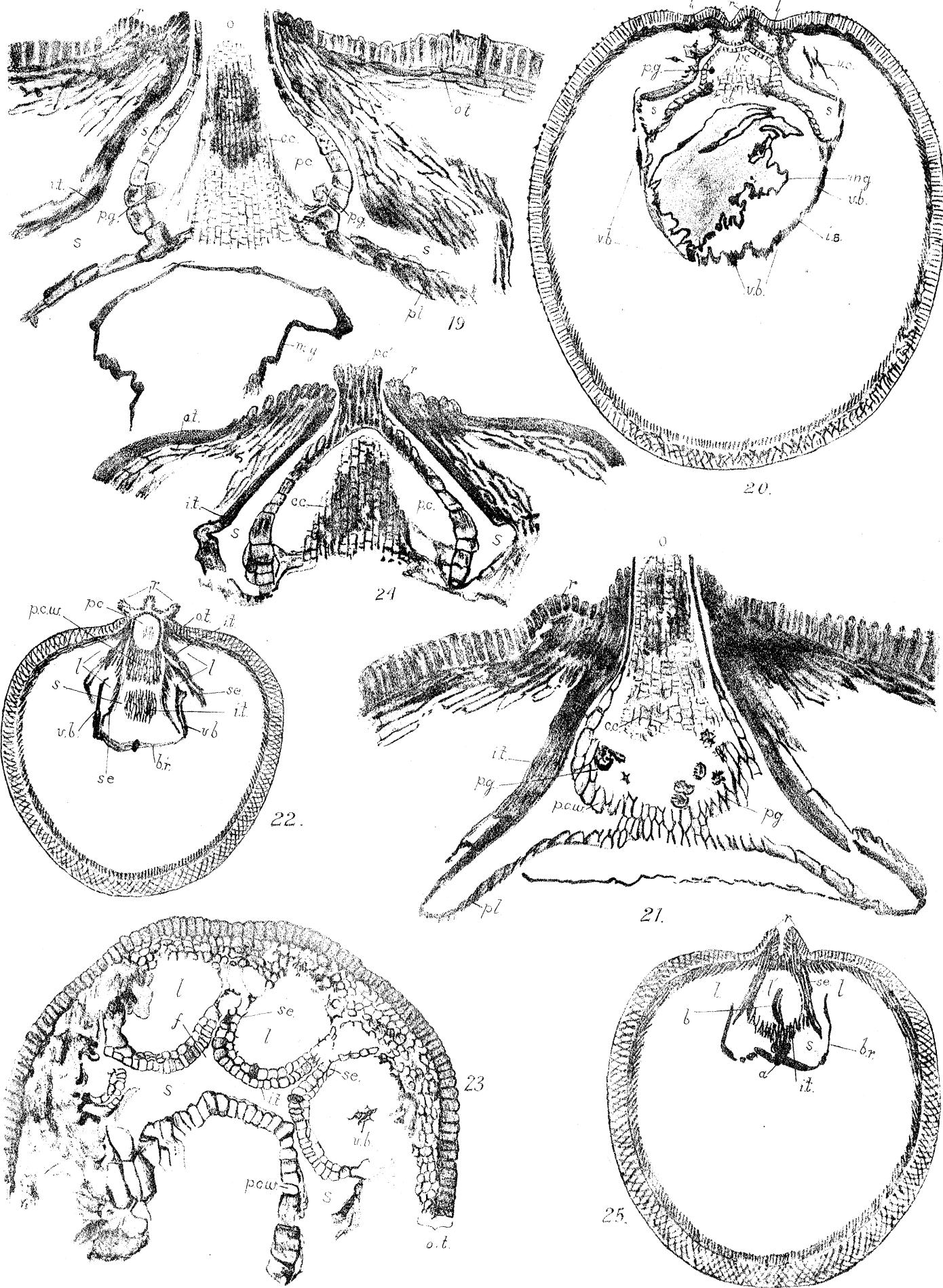


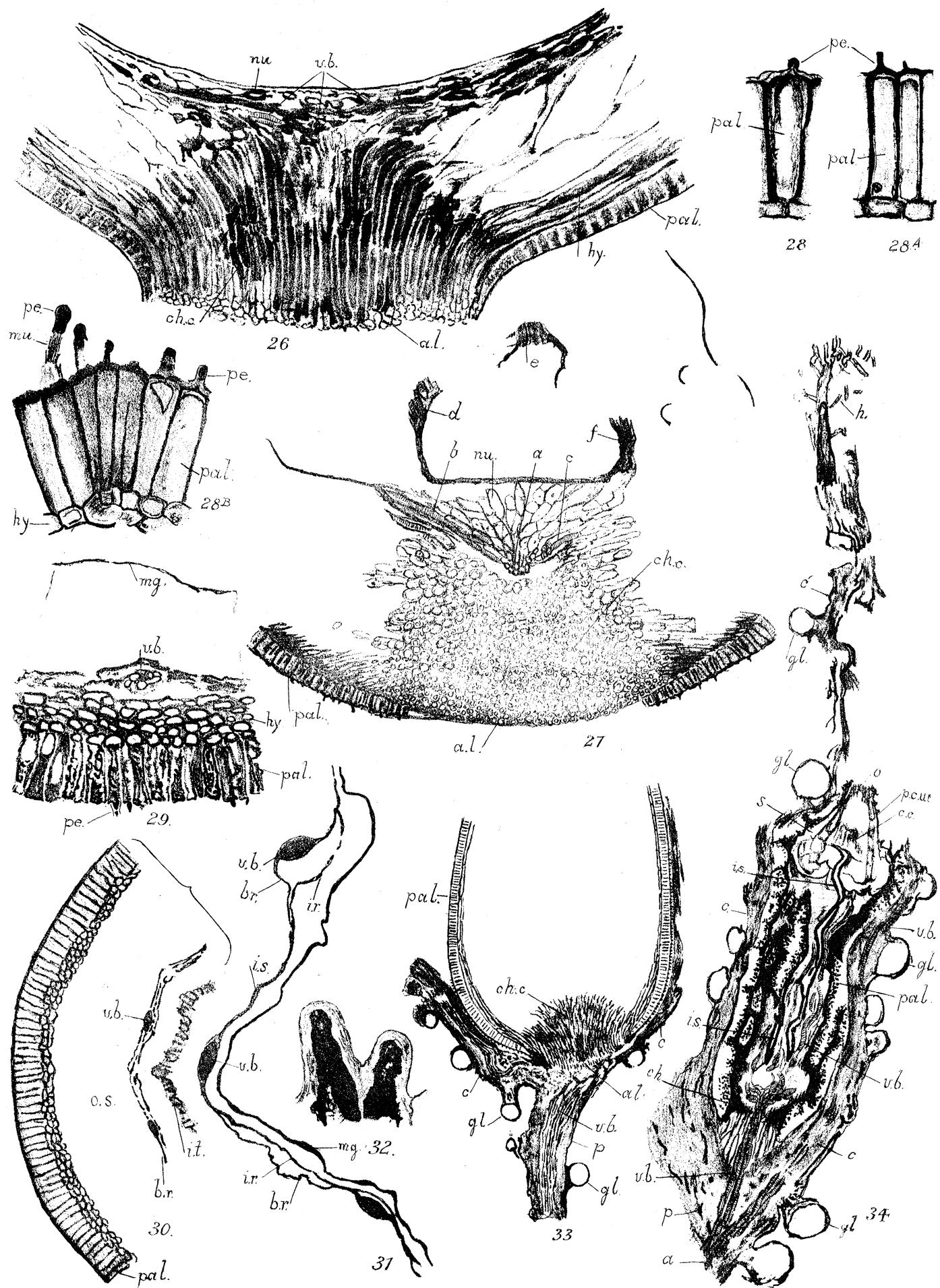
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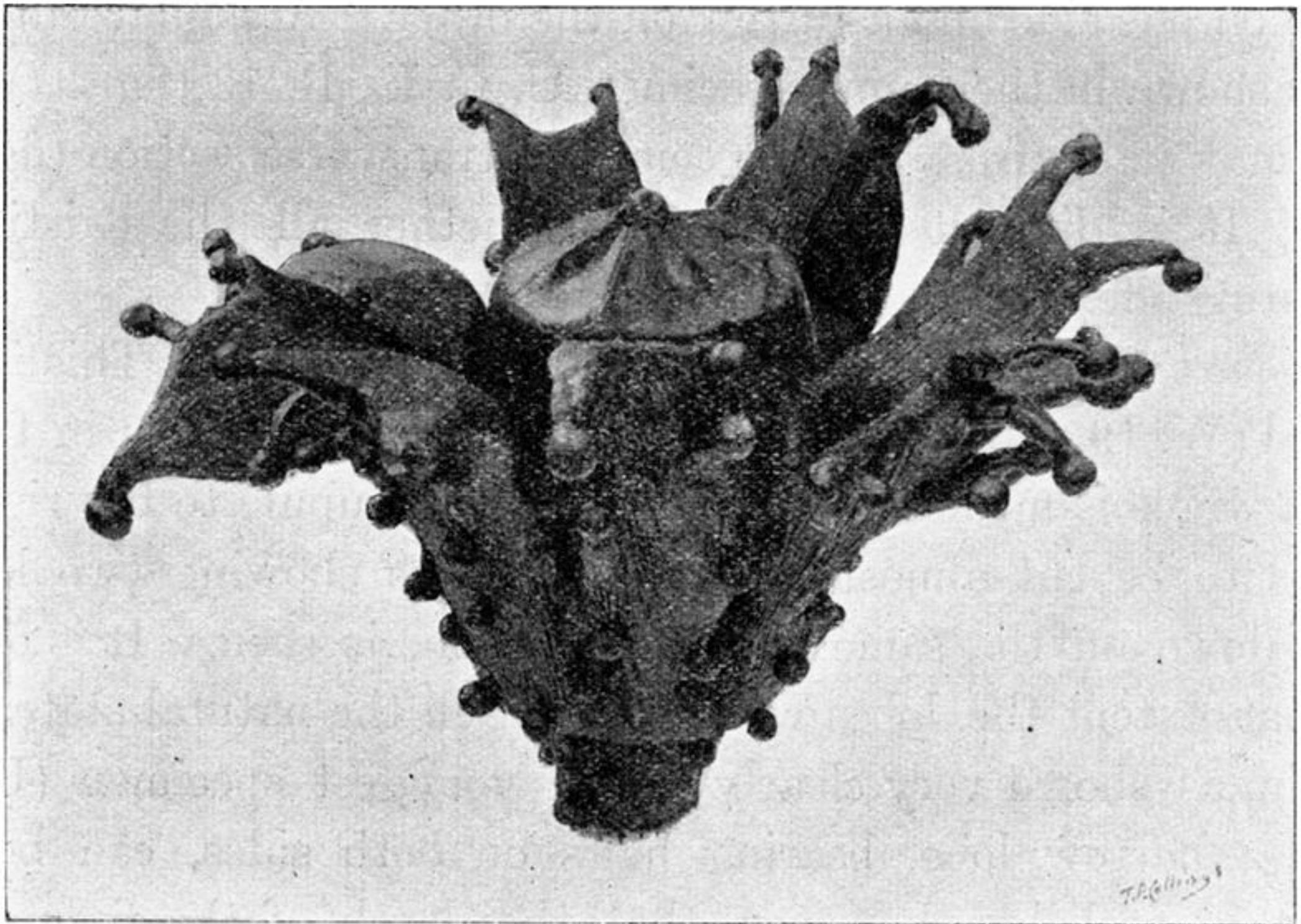




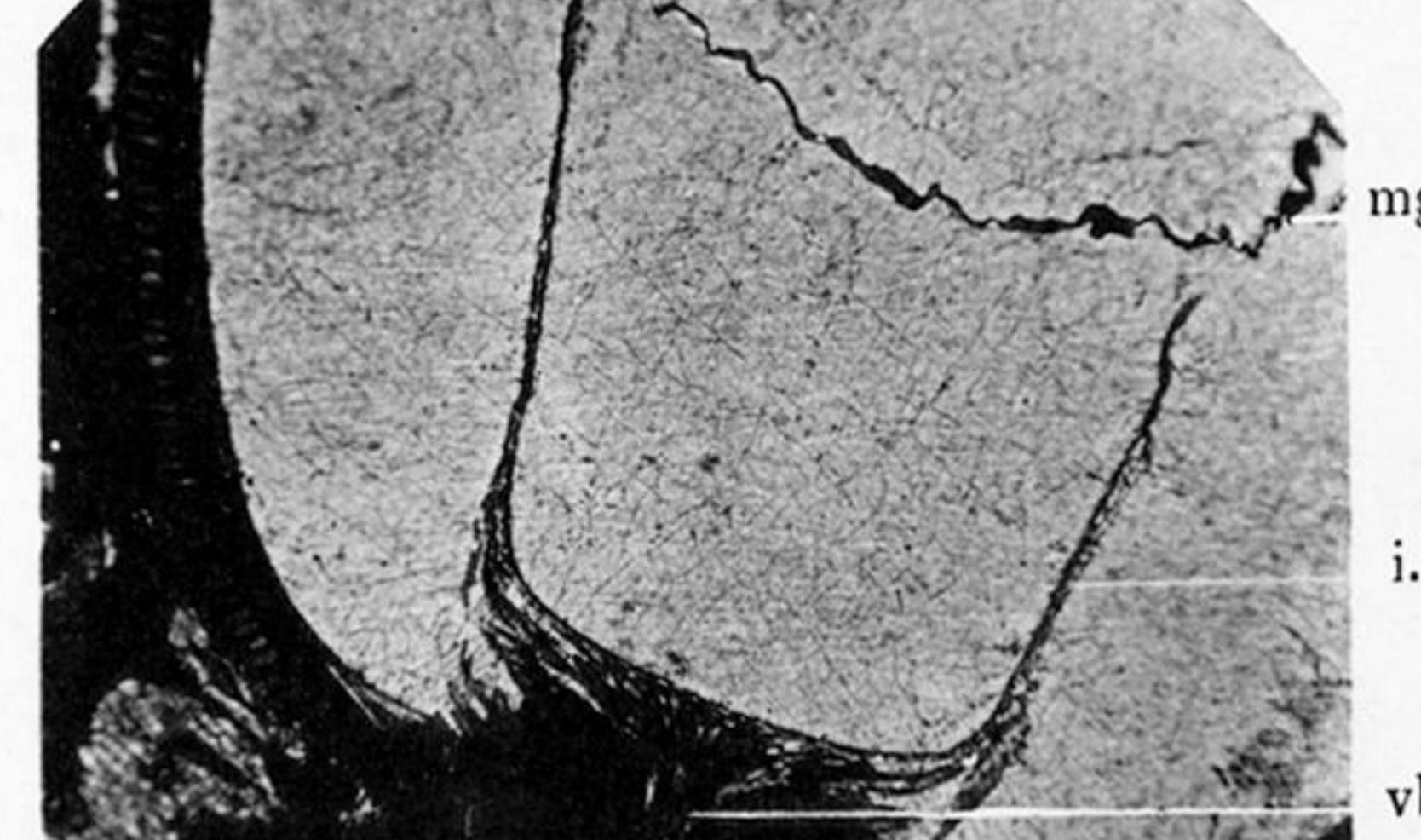
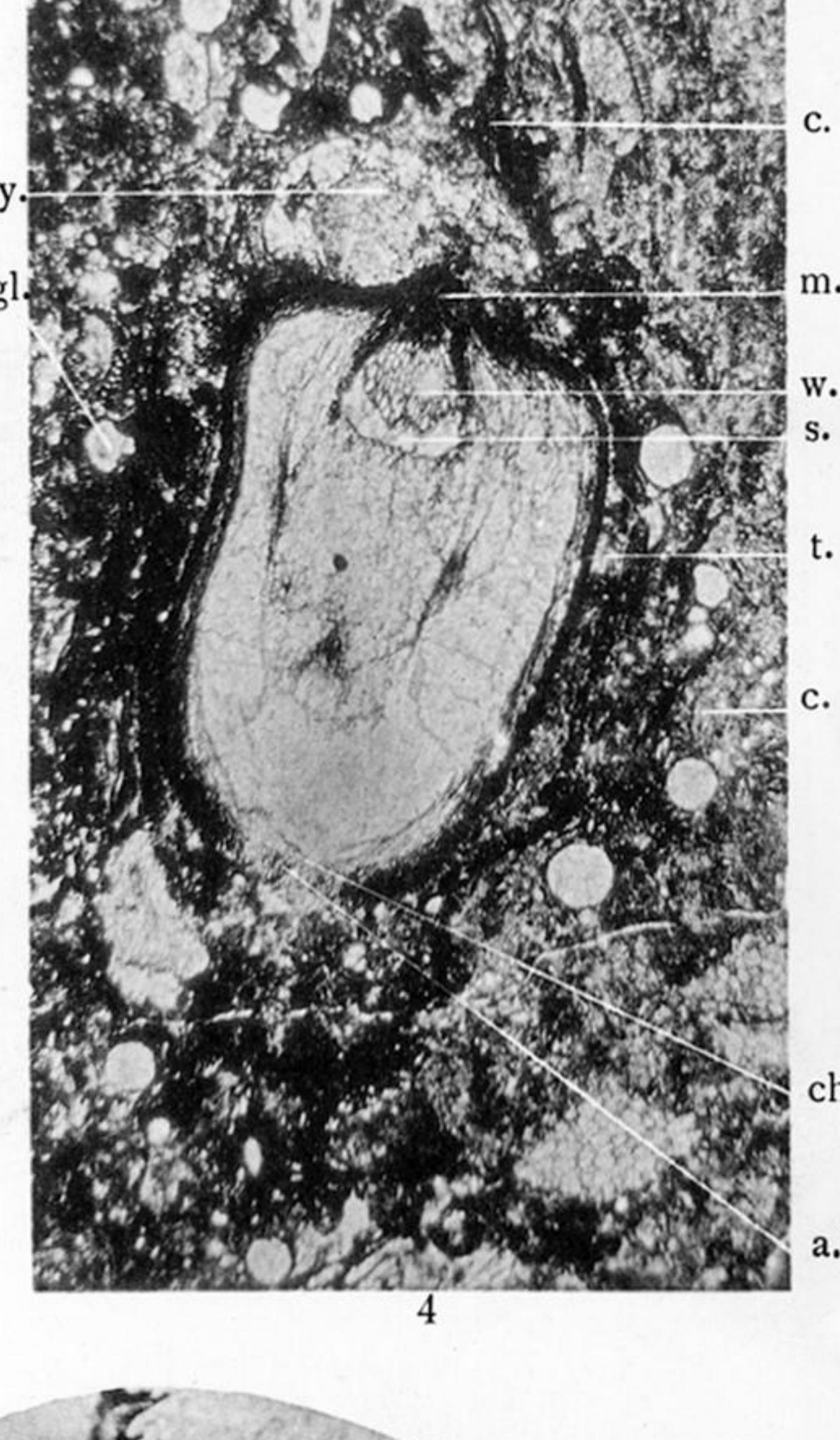
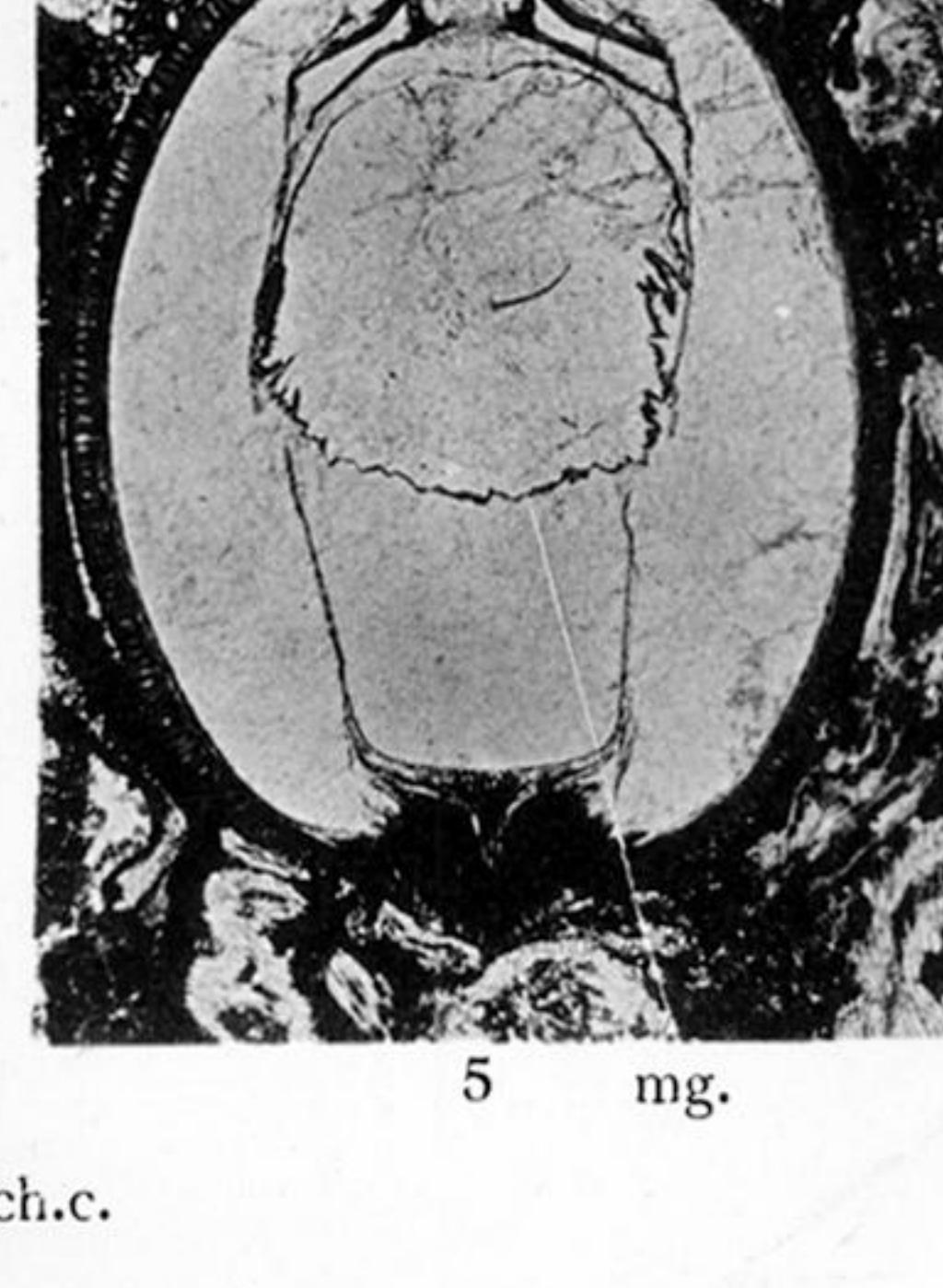
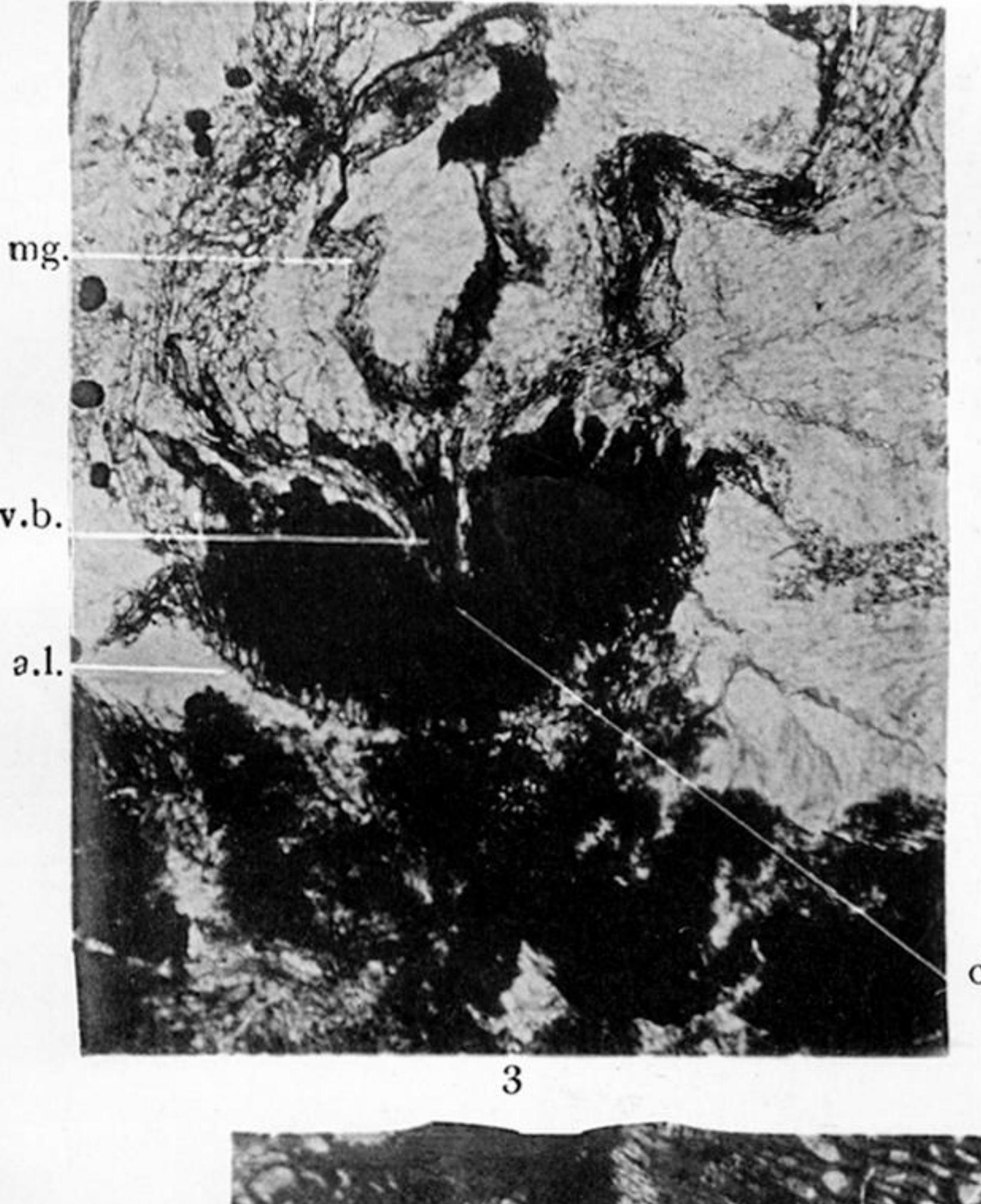
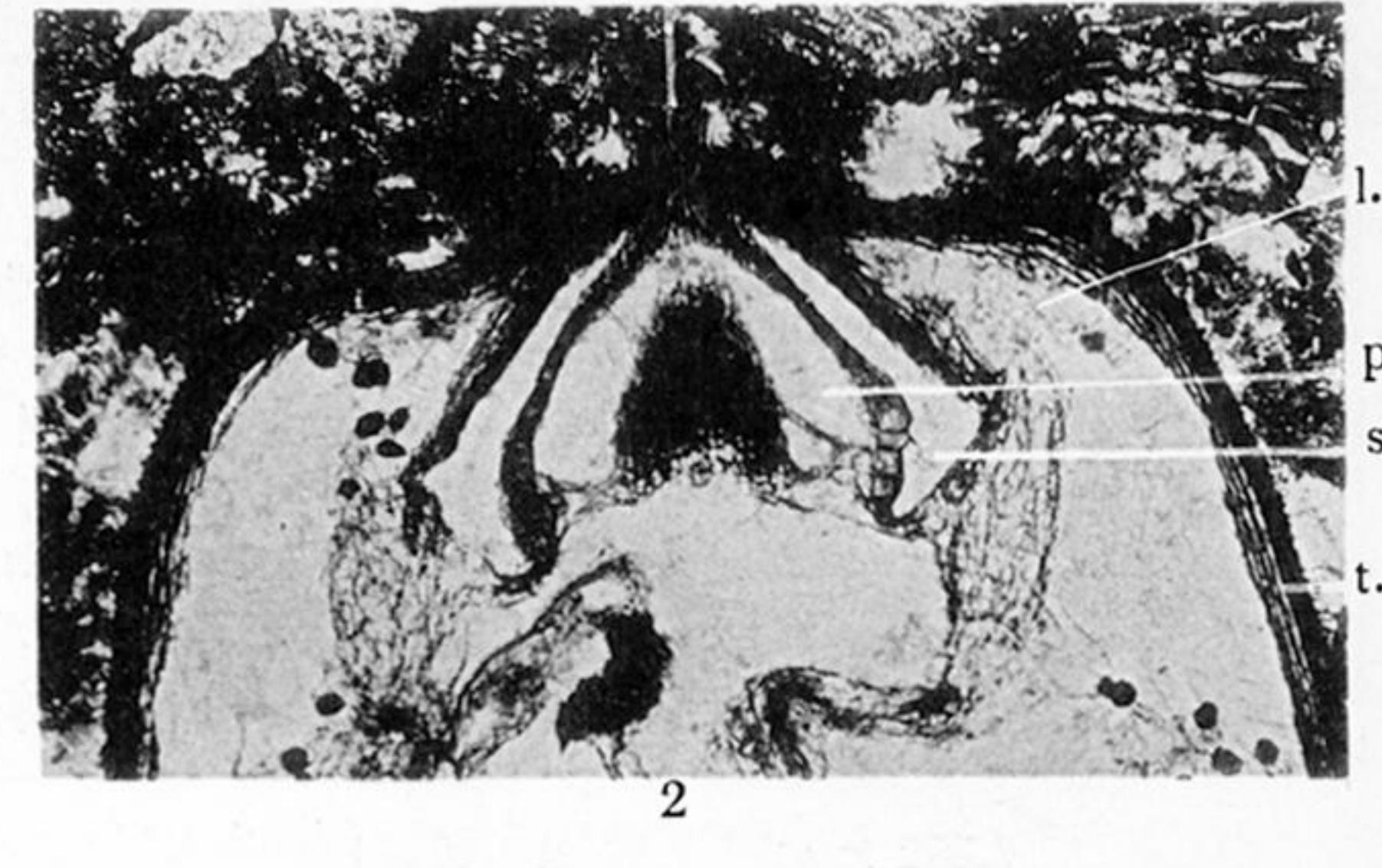
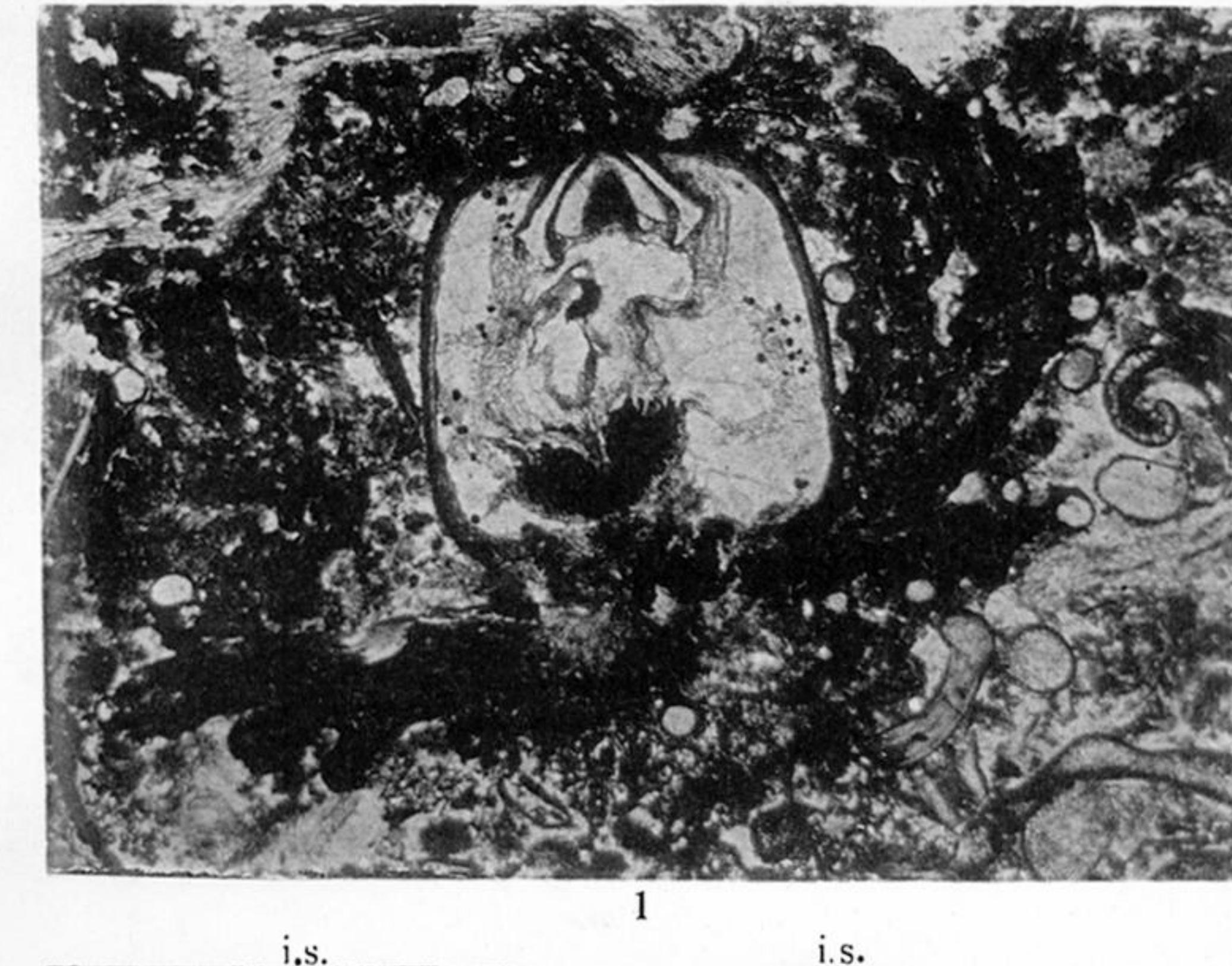








TEXT-FIG. 2.—Photograph from a large Wax Model of a Restoration of a small-sized Seed of *Lagenostoma Lomari*, enclosed in its Cupule. Model prepared by Mr. H. E. H. SMEDLEY.



LAGENOSTOMA LOMAXI.

Plates 4-6.—Photographs from the sections. In most cases they should be examined with the aid of a hand-lens. Photographs 1-7 and 14-27 are by Mr. L. A. BOODLE. Photographs 8-13 by Mr. W. TAMS, of Cambridge.

PLATE 4.

Phot. 1.—Longitudinal section of a small arrested seed enclosed in its cupule, which loosely invests it on all sides. The cupule bears numerous glands with hollow heads. In the seed the testa, chalaza, canopy, pollen-chamber, and other parts are seen, as shown more in detail in photos. 2 and 3.

W. 1931, A. \times about 15. (See pp. 211 and 216.)

Phot. 2.—Upper part of the same seed. *t.*, testa, consisting of young palisade layer and hypoderm: *l.*, a loculus of the canopy; *s.*, sinus, or space between inner wall of canopy and wall of pollen-chamber; *p. c.*, the bell-shaped pollen-chamber surrounding the central cone, which is not quite in median section; *p. c.'*, tube of chamber, projecting beyond the micropyle.

W. 1931, A. \times about 36. (See p. 200.)

Phot. 3.—Lower part of the same seed, slightly overlapping the part shown in phot. 2. *a. l.*, abscission-layer; *ch. c.*, the bulky chalazal cushion, displaced upwards, as seen in phot. 1; *v. b.*, vascular bundle of chalaza, branching out above into bundles which traverse the contracted intermediate sac, *i. s.*; *mg.*, membrane of megasporangium, which is seen complete, but contracted.

W. 1931, A. \times about 45. (See p. 212.)

Phot. 4.—Another small cupulate seed, in tangential section. *c.*, cupule, bearing many glands; *gl.*, the gland represented in phot. 22. Above the seed the cupule encloses a pinnule of *Lyginodendron*, *Ly.*; *a. l.*, abscission-layer; *ch.*, chalaza; *t.*, testa, with conspicuous hypoderm; *s.*, sinus; *w.*, wall of pollen-chamber in tangential section; *m.*, micropyle. In the body of the seed three vascular bundles are seen.

W. 1931. \times about 20. (See pp. 211, 212.)

Phot. 5.—Full-sized seed in longitudinal section. At the chalazal end the section is fairly median, but at the micropylar end it misses the central cone of the pollen-chamber. Otherwise all the parts of the seed are shown, as represented in detail in photos. 6 and 7. *mg.*, contracted membrane of megasporangium.

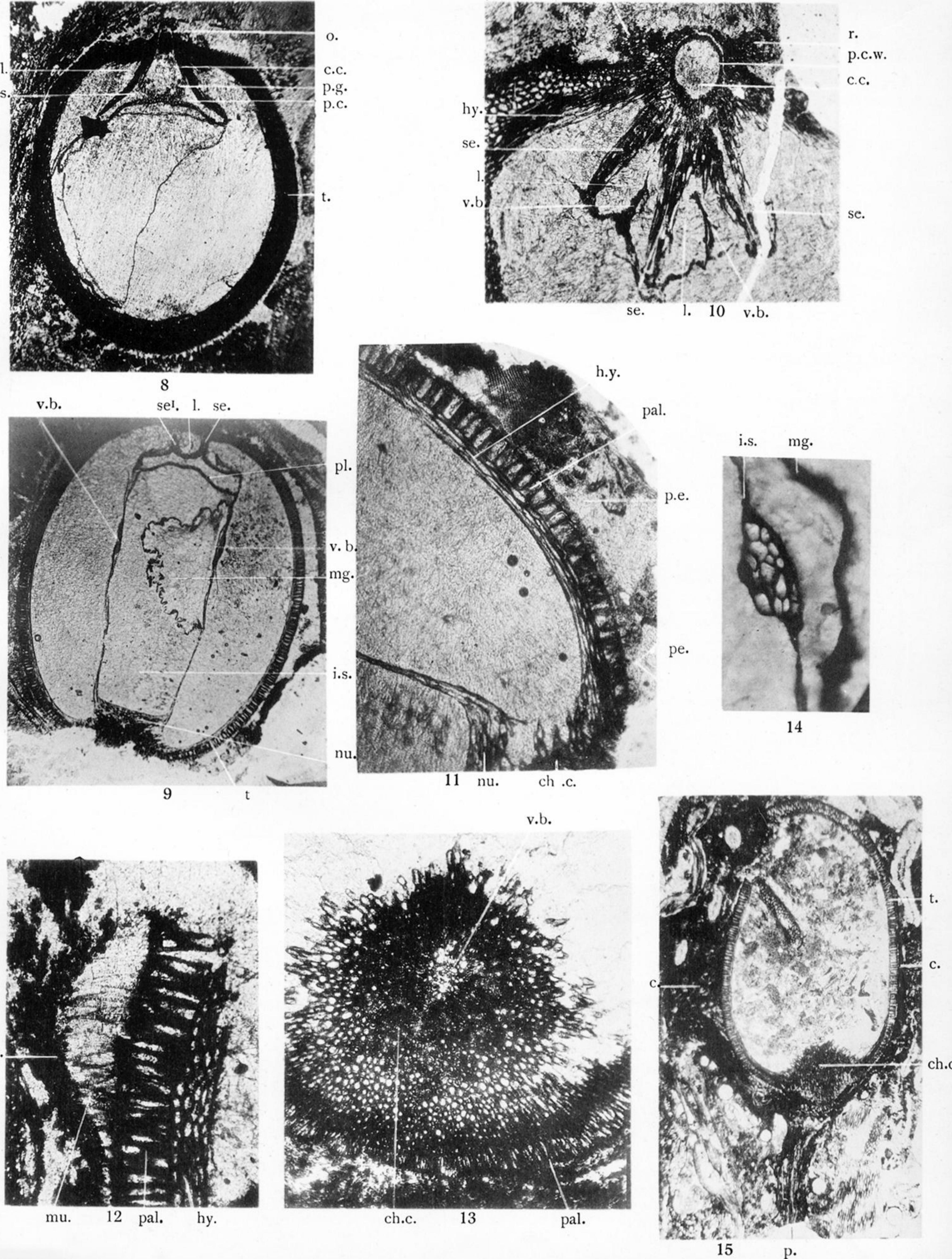
W. 1930. \times about 10. (See p. 198.)

Phot. 6.—Upper part of the same seed. *pal.*, palisade layer of testa; *o. t.*, outer, *i. t.*, inner wall of canopy, the loculus between them contains some remains of tissue; *s.*, sinus; *w.*, wall of pollen-chamber, projecting slightly beyond micropyle at *p. c.'*; *mg.*, membrane of megasporangium, within which remains of prothallial tissue are seen.

W. 1930. \times about 26. (See p. 200.)

Phot. 7.—Lower part of the same seed. *a. l.*, abscission-layer; *ch. c.*, chalazal cushion; *v. b.*, vascular bundle of chalaza (cf. Plate 7, fig. 5); *i. s.*, intermediate sac; *mg.*, membrane of megasporangium contracted.

W. 1930. \times about 26. (See p. 207.)



LAGENOSTOMA LOMAXI.

PLATE 5.

Phot. 8.—Slightly oblique longitudinal section of a full-sized seed. The pollen-chamber (*p. c.*) is cut in a tangential plane and shows two groups of pollen-grains (*p. g.*). *c.c.*, central cone of pollen-chamber; *o.*, orifice of pollen-chamber; *s.*, sinus round the pollen-chamber; *l.*, loculus of canopy; *t.*, testa. The lower end of the section falls outside the abscission-layer. The pollen-chamber of this specimen is enlarged in Plate 9, fig. 21.

U. C. L., R. 2. \times about 16. (See p. 200.)

Phot. 9.—Longitudinal section of a full-sized seed. The section falls outside the pollen-chamber at the apex, but approaches the axis of the seed in its lower part. *se.*, *se'*, complete and incomplete septa of canopy; *l.*, loculus of canopy; *pl.*, plinth or mound upon the summit of which the pollen-chamber stands; *i. s.*, intermediate sack contracted; *v. b.*, *v. b.*, vascular bundles; *mg.*, contracted membrane of megasporangium containing prothallial tissue; *nu.*, tissue at base of nucellus.

U. C. L., R. 3, *a.* \times about 13. (See p. 203.)

Phot. 10.—Very oblique section across the top of a full-sized seed, cutting two of the loculi of the canopy tangentially in the plane of the vascular bundles. *p. c. w.*, wall of pollen-chamber; *c.c.*, central cone of pollen-chamber; *l.*, *l.*, loculi of canopy cut in tangential section; *v. b.*, *v. b.*, vascular bundles of these loculi, abutting below on the bundle-ring; *se.*, *se.*, septa separating the loculi; *pal.*, *hy.*, palisade and hypodermal layers of testa; *r.*, *r.*, ridge around the micropyle, cut obliquely.

U. C. L., R. 9, *c.* \times about 40. (See p. 204.)

Phot. 11.—Testa from specimen in phot. 9 (right hand, at base), more highly magnified, and rotated through 90°. *pal.*, palisade-layer bearing pegs (*pe.*, *pe.*) with normal preservation; *hy.*, hypoderm of testa; *nu.*, tissue at base of nucellus; *ch. c.*, chalazal cushion.

U. C. L., R. 3, *a.* \times about 46. (See p. 206.)

Phot. 12.—Transverse section of testa of full-sized seed, with palisade cells and mucilage cones. *pal.*, palisade cells; *mu.*, mucilage cones; *pe.*, position of peg raised on a mucilage cone; *hy.*, hypoderm of testa.

U. C. L., R. 8, *b.* \times about 100. (See p. 206.)

Phot. 13.—Approximately transverse section of the chalaza of a full-sized seed with chalazal vascular bundle (testa shown on *lower* side of photograph only). *v. b.*, vascular bundle; *ch. c.*, chalazal cushion; *pal.*, palisade-layer of testa.

U. C. L., R. 8, *a.* \times about 45. (See p. 208.)

Phot. 14.—Transverse section of one of the vascular bundles of the seed (that marked *v. b.* in Plate 7, fig. 2). *i. s.*, part of the "intermediate sack" on which the bundle abuts; *mg.*, part of the megasporangium membrane. In the bundle only the xylem is evident; the smaller elements are on the whole directed towards the inner side.

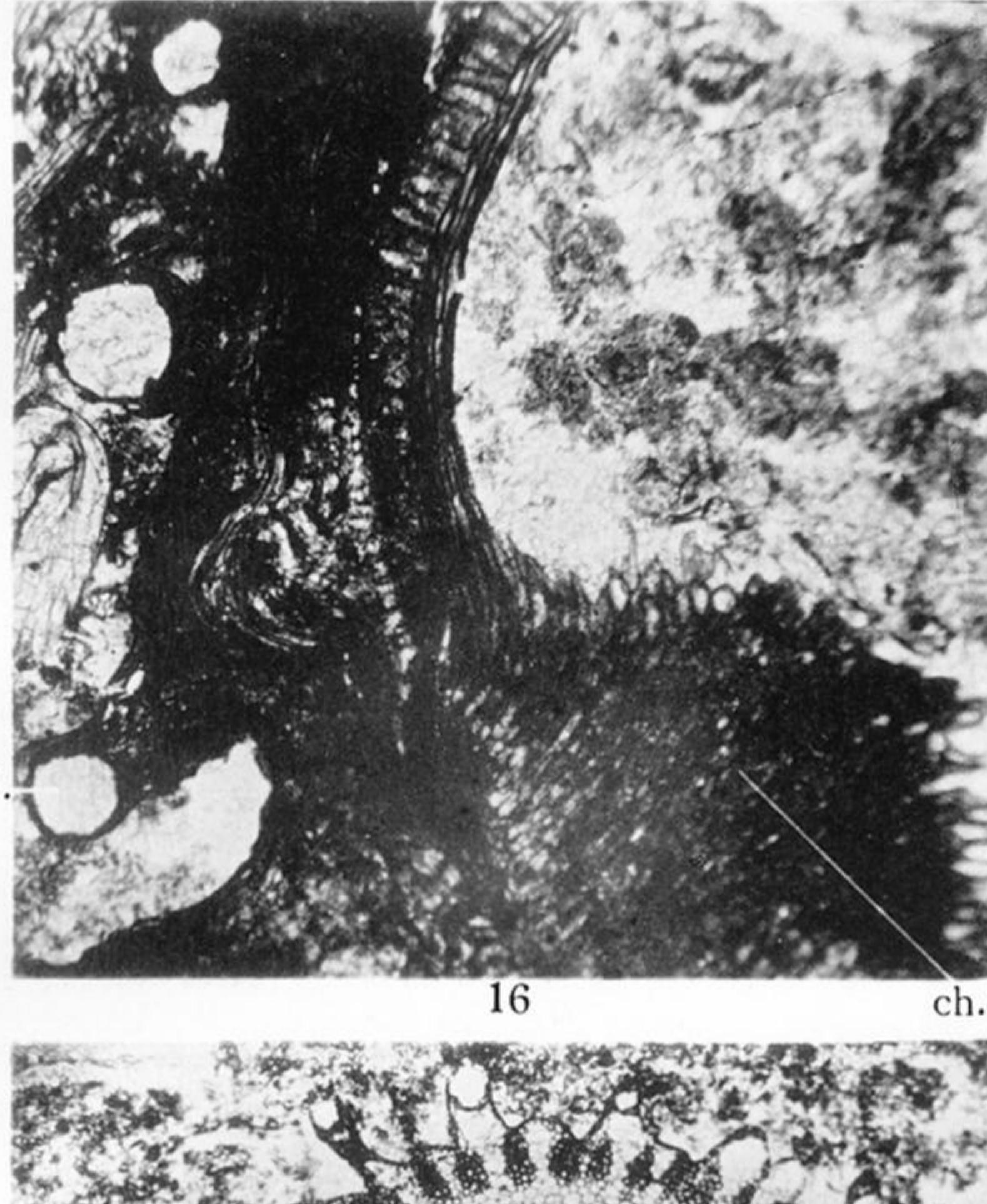
W. 1915, O. \times about 200. (See p. 210.)

Phot. 15.—Longitudinal section of cupulate seed and pedicel. The section is obliquely tangential, approaching the median plane at the lower end. *p.*, pedicel on which the seed is borne; *c. c.*, cupule bearing glands; on each side it extends a little above the reference-line; *t.*, testa of seed; *ch. c.*, chalazal cushion. Cf. Plate 10, fig. 22. Portions of the seed are shown enlarged in photos. 16 and 21.

S. 558. \times 13. (See p. 217.)

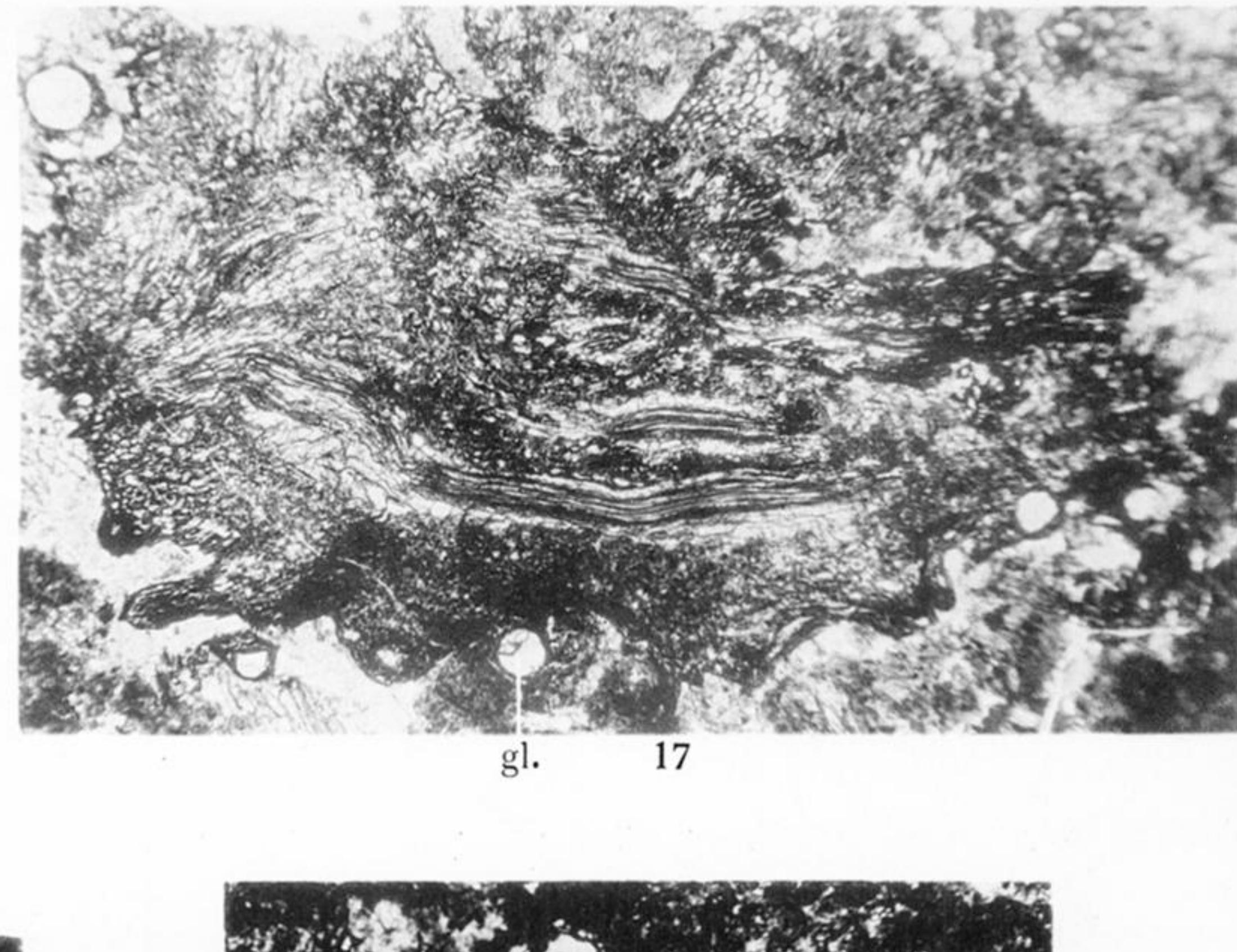
c

pal. hy.



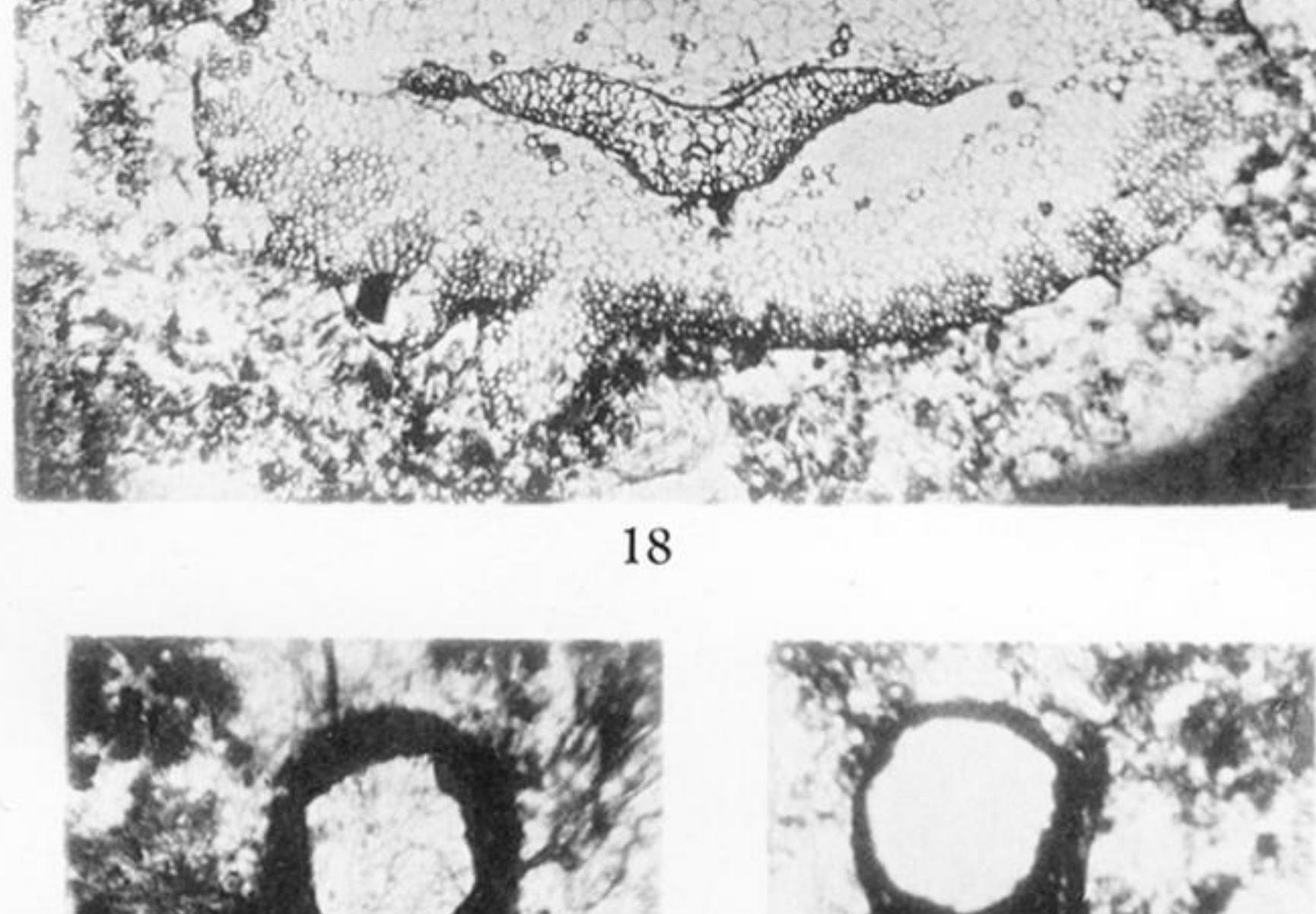
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ch.c.



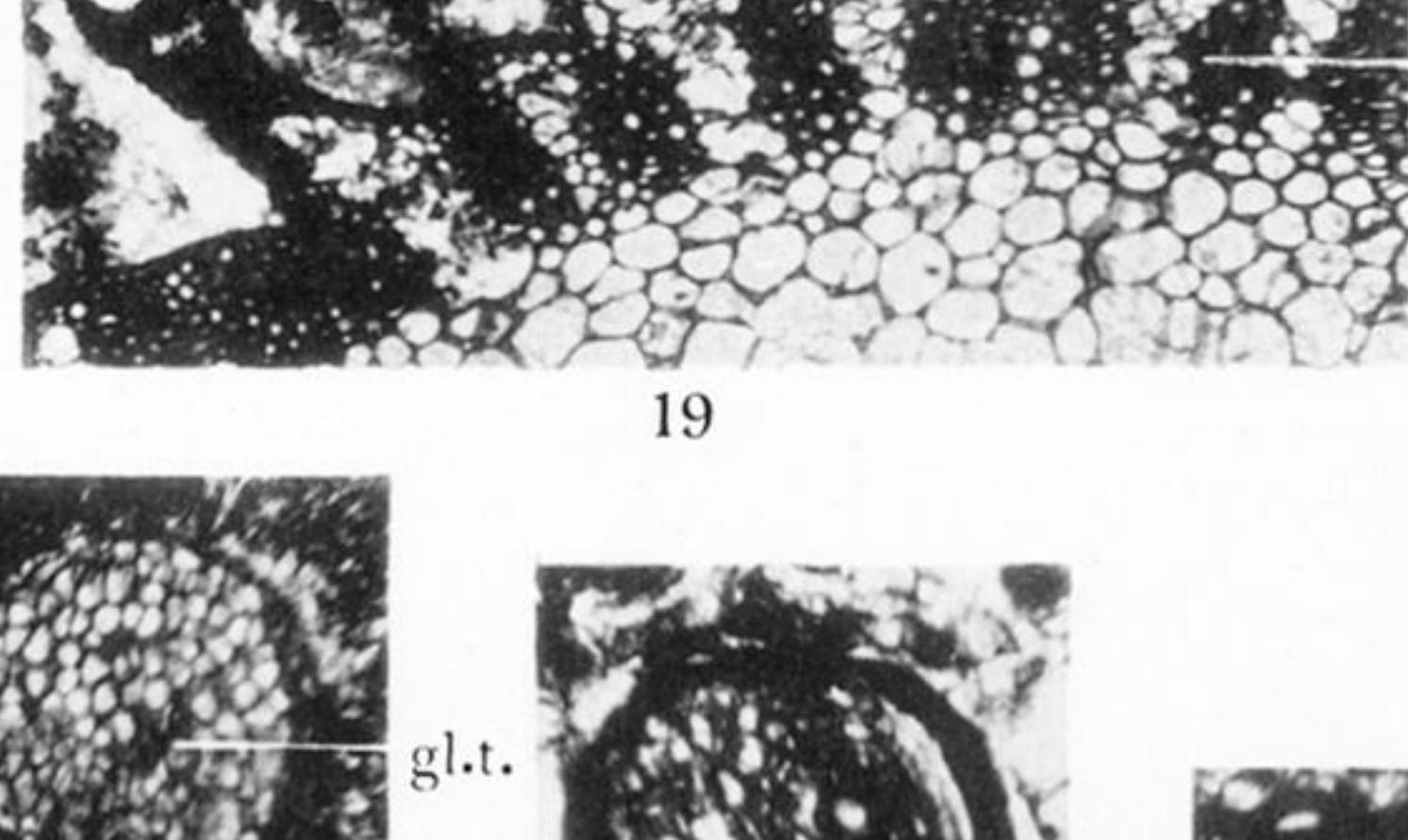
gl.

17



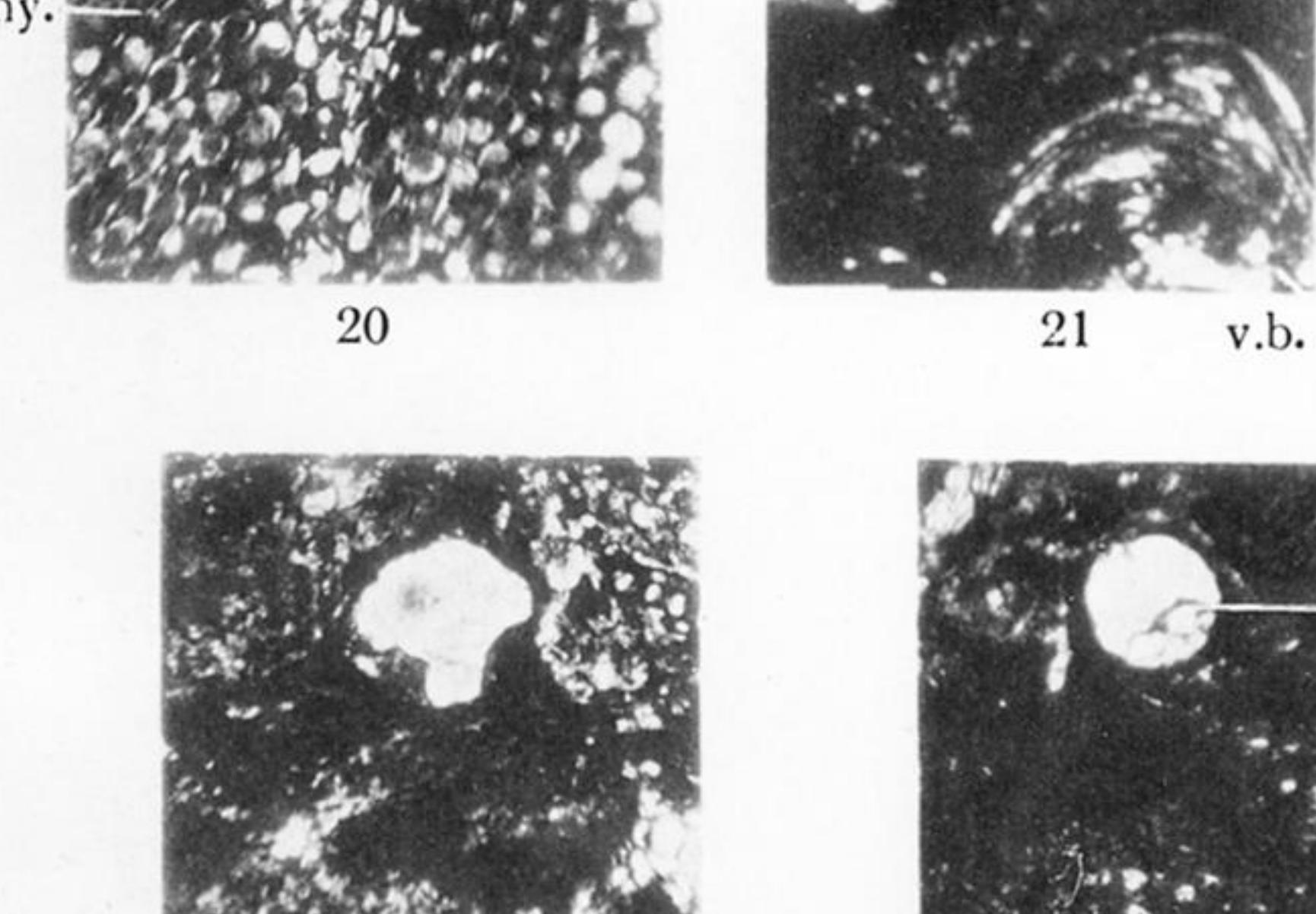
18

ch.c.

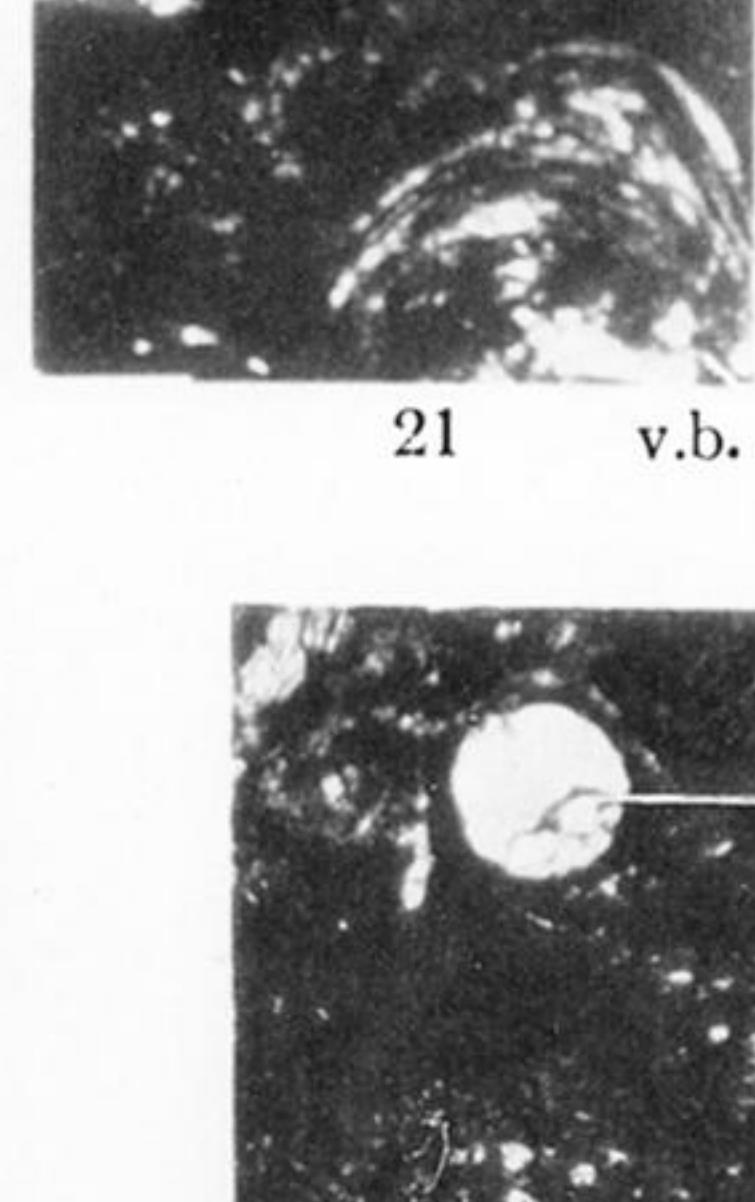


19

hy.

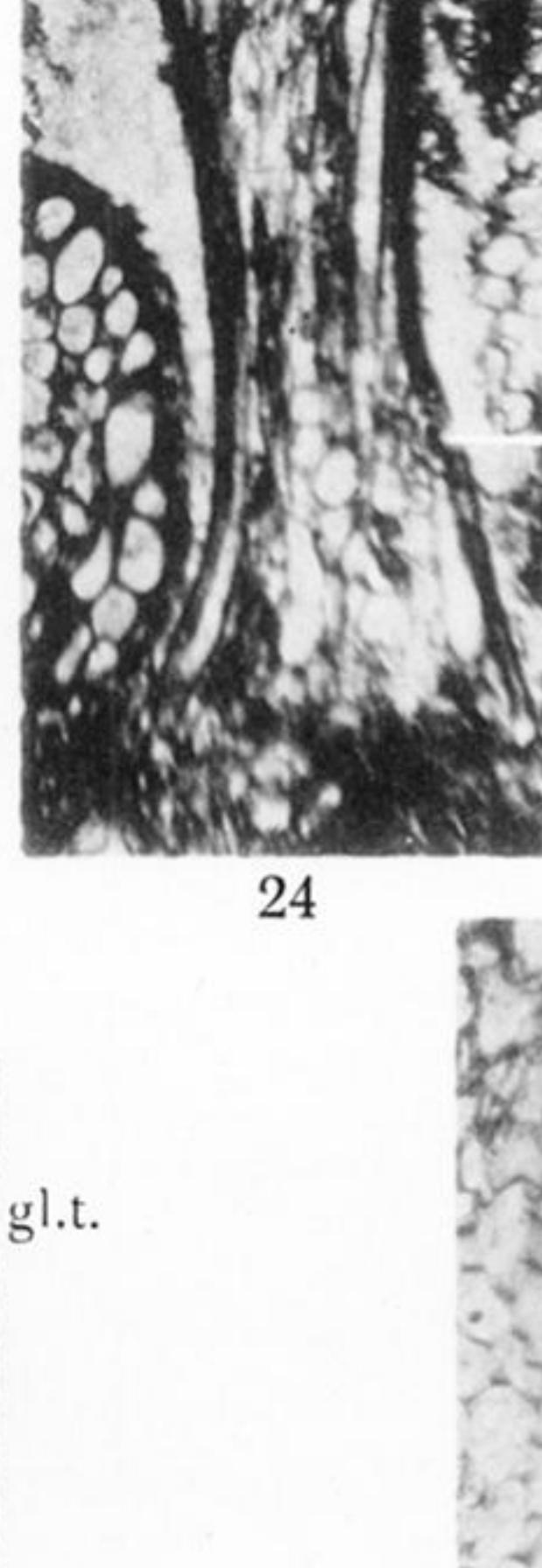


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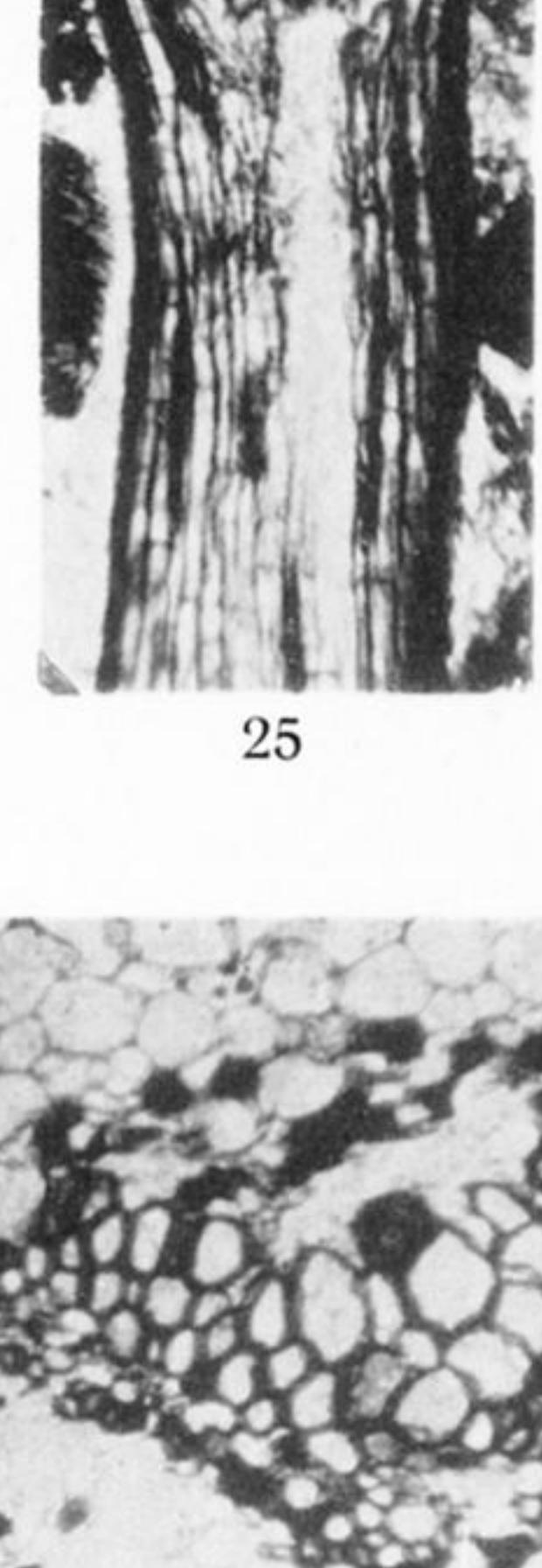


21

v.b.

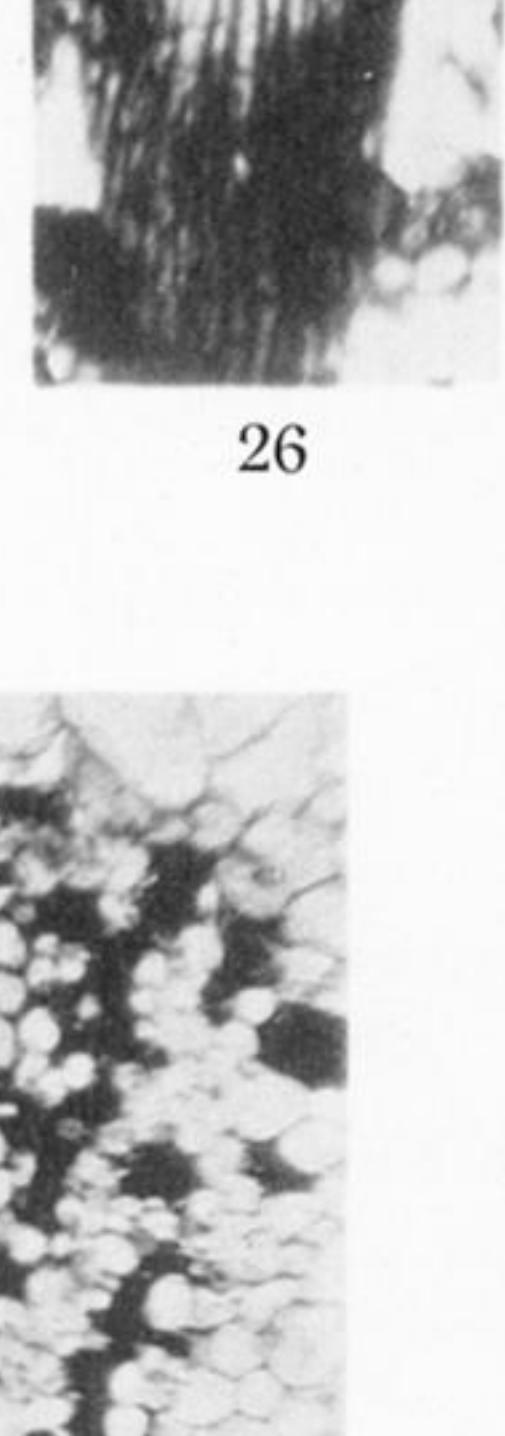


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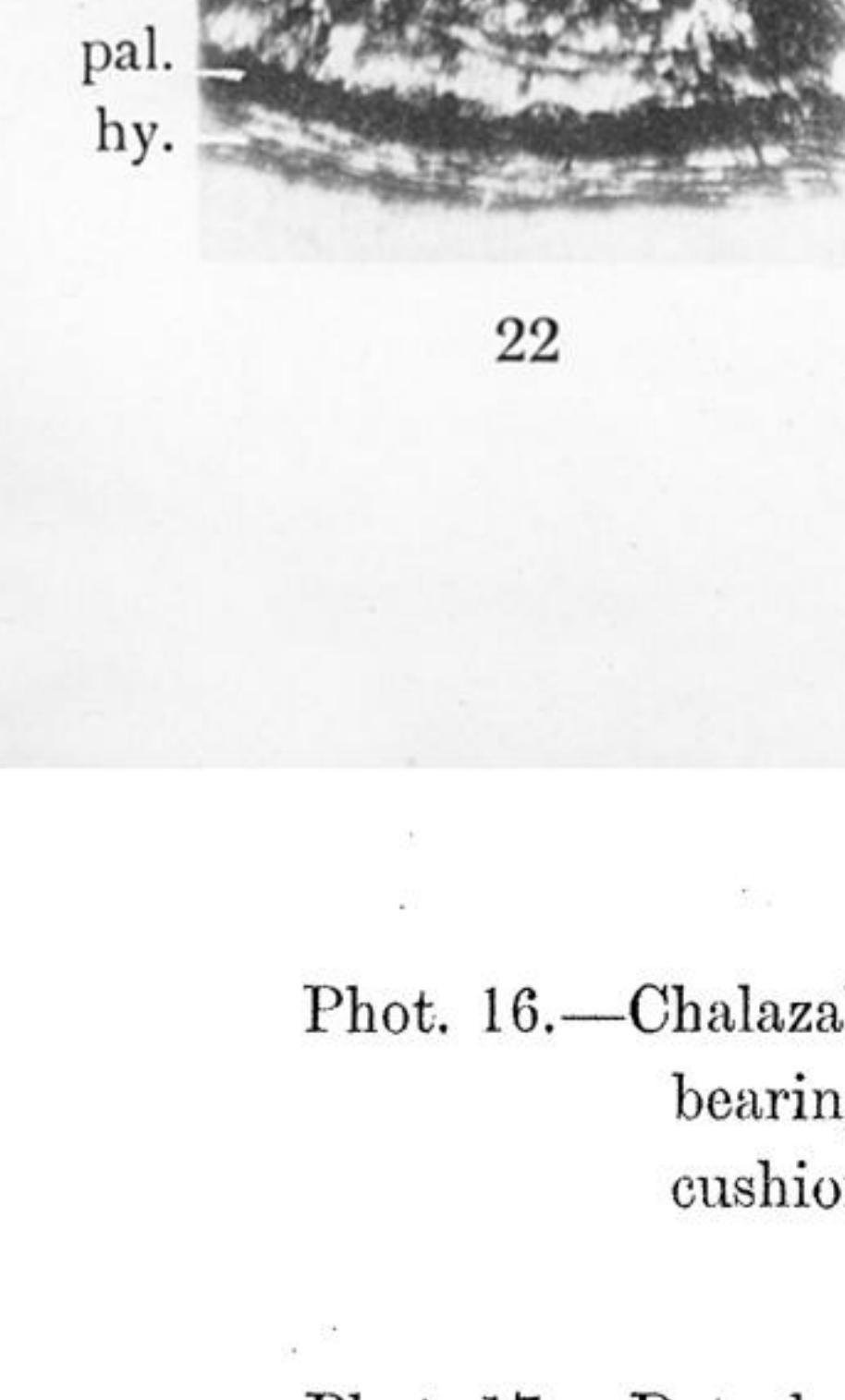
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gl.t.

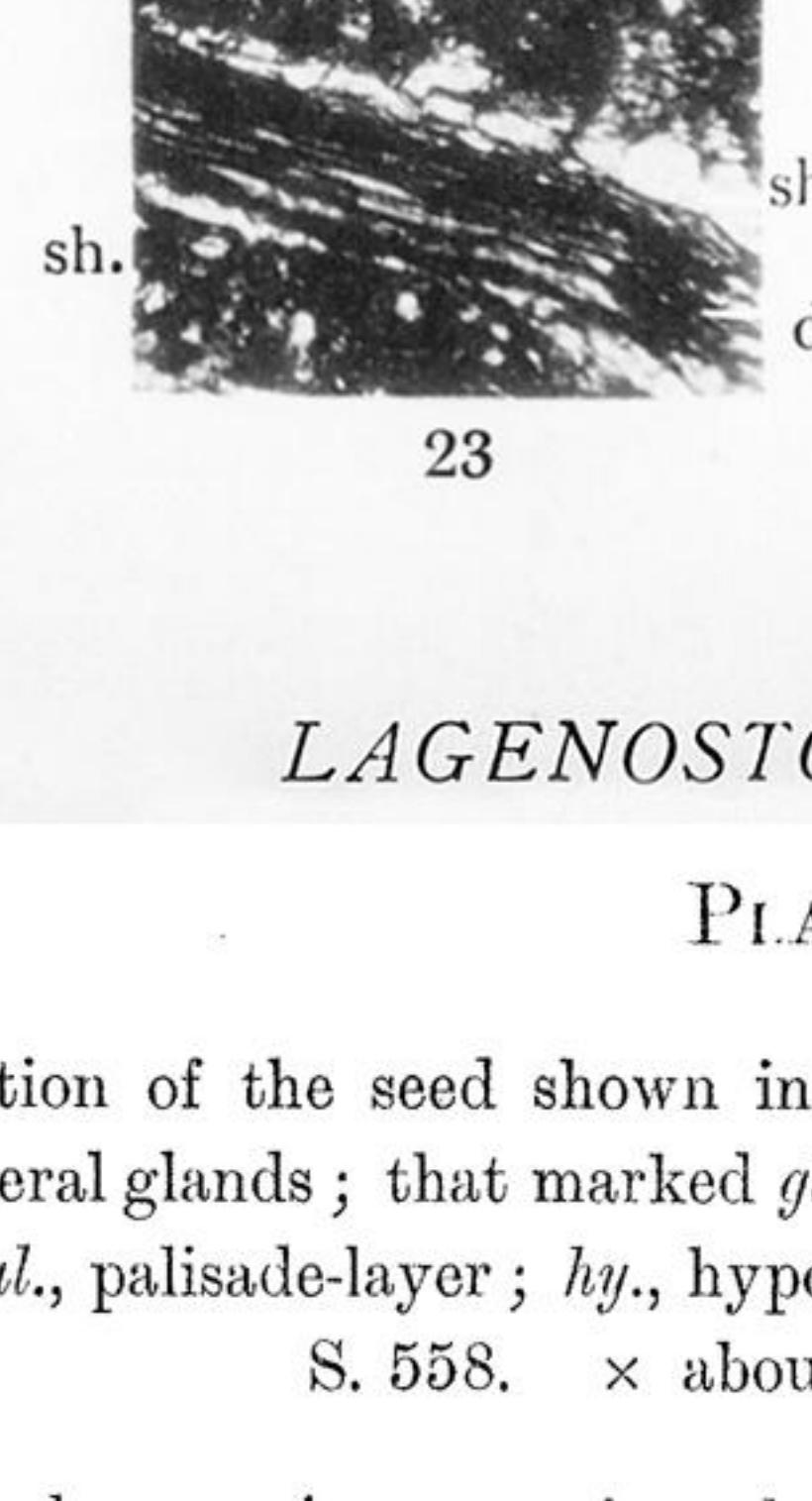


26

gl.t.



22

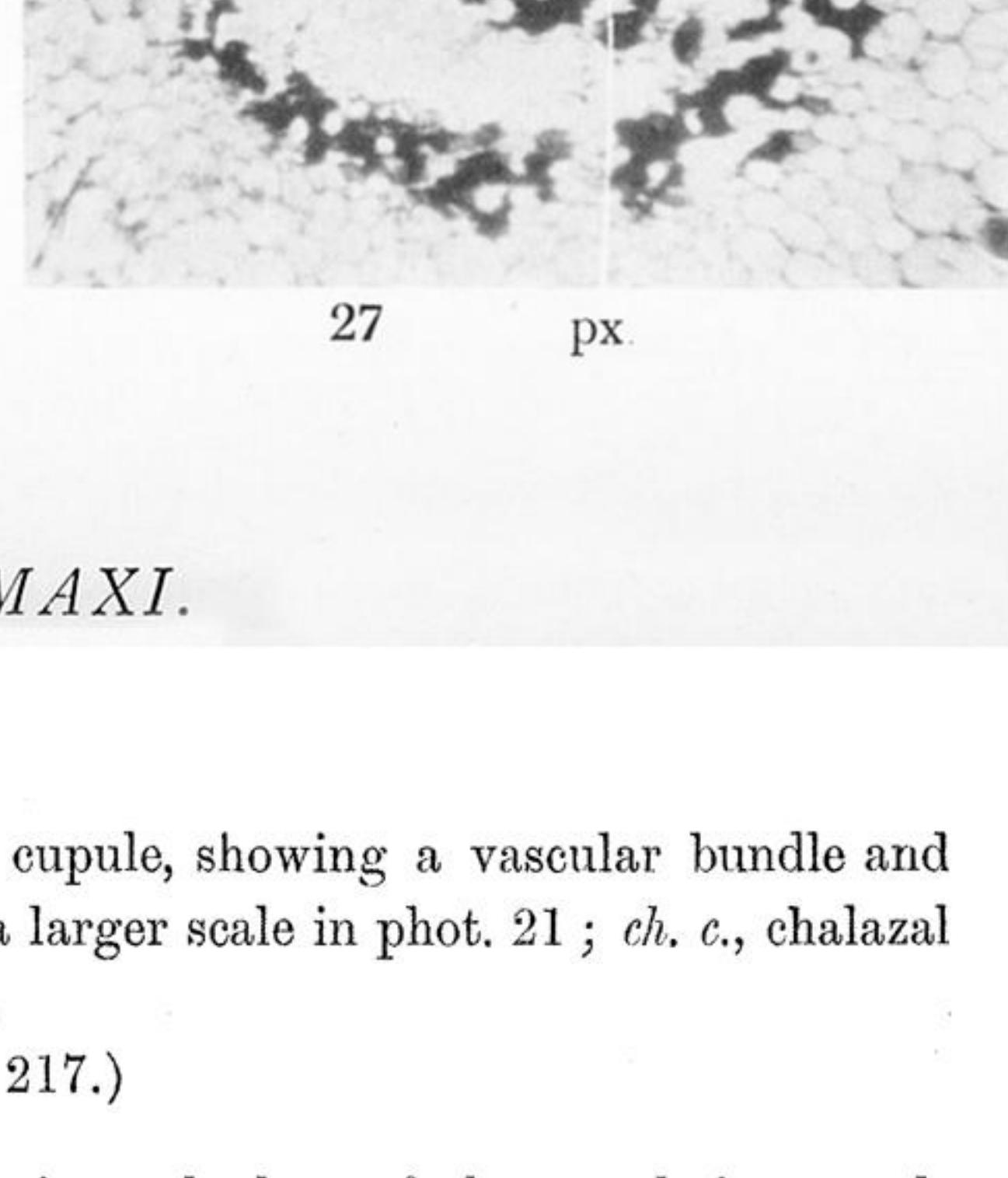


23

gl.t.

sh.

d.



27

px.

LAGENOSTOMA LOMAXI.

PLATE 6.

Phot. 16.—Chalazal portion of the seed shown in phot. 15. *c.*, cupule, showing a vascular bundle and bearing several glands; that marked *gl.* is shown on a larger scale in phot. 21; *ch. c.*, chalazal cushion; *pal.*, palisade-layer; *hy.*, hypoderm of testa.

S. 558. \times about 35. (See p. 217.)

Phot. 17.—Detached cupule, seen in approximately tangential section; the base of the cupule is towards the left; several glands are shown; that marked *gl.* is represented further enlarged in phot. 23. The course of the bundles traversing the cupule is shown in the semi-diagrammatic fig. 11, Plate 8.

U. C. L., R. 14, *a.* \times 28. (See p. 219.)

Phot. 18.—Transverse section of a small petiole of *Lyginodendron Oldhamium*, showing the characteristic vascular bundle and hypoderm. Numerous glands are present, in three of which the head is seen to be hollow; *cf.* phot. 19.

S. 625. \times 15. (See p. 227.)

Phot. 19.—Portion of the same petiole enlarged, showing the three glands with the head in the hollow state of preservation. *hy.*, hypoderm, with radial sclerotic bands.

S. 625. \times 36. (See p. 227.)

Phot. 20.—Gland from another section of the same petiole, for comparison with the gland shown in phot. 21 from the cupule of *Lagenostoma Lomaxi*. The head of the gland is completely empty, while the tissue of the stalk is well preserved. *hy.*, sclerotic band of hypoderm.

U. C. L., M. 11, *c.* \times 70. (See p. 227.)

Phot. 21.—Gland (marked *gl.* in phot. 16) from the cupule of *Lagenostoma Lomaxi*, for comparison with the petiolar gland shown in phot. 20. *v. b.*, a vascular bundle of the cupule.

S. 558. \times 70. (See pp. 223 and 227.)

Phot. 22.—Gland (marked *gl.* in phot. 4) on the cupule of a small seed. Note the pear-shaped cavity of the head. *c.*, cupule; *pal.*, palisade-layer; and *hy.*, hypoderm of the testa of the seed.

W. 1931. \times 54. (See p. 224.)

Phot. 23.—Gland (marked *gl.* in phot. 17) from a cupule. *gl. t.*, remains of glandular tissue in the cavity of the head. Below, a part of the vascular bundle *d.* (see Plate 8, fig. 11) is seen. *sh.*, *sh.*, large-celled bundle-sheath.

U. C. L., R. 14, *a.* \times about 60. (See p. 223.)

Phot. 24.—Detached vegetative gland, to show the typical structure. Compare Plate 8, fig. 18, where a similar though longer gland is shown *in situ* on the stem. *gl. t.*, glandular tissue of the head, almost perfectly preserved. The structure of the stalk is also well shown. *st.*, depressed stoma.

S. 447. \times about 60. (See p. 226.)

Phot. 25.—Detached vegetative gland. The glandular tissue, *gl. t.*, has here become somewhat disorganized.

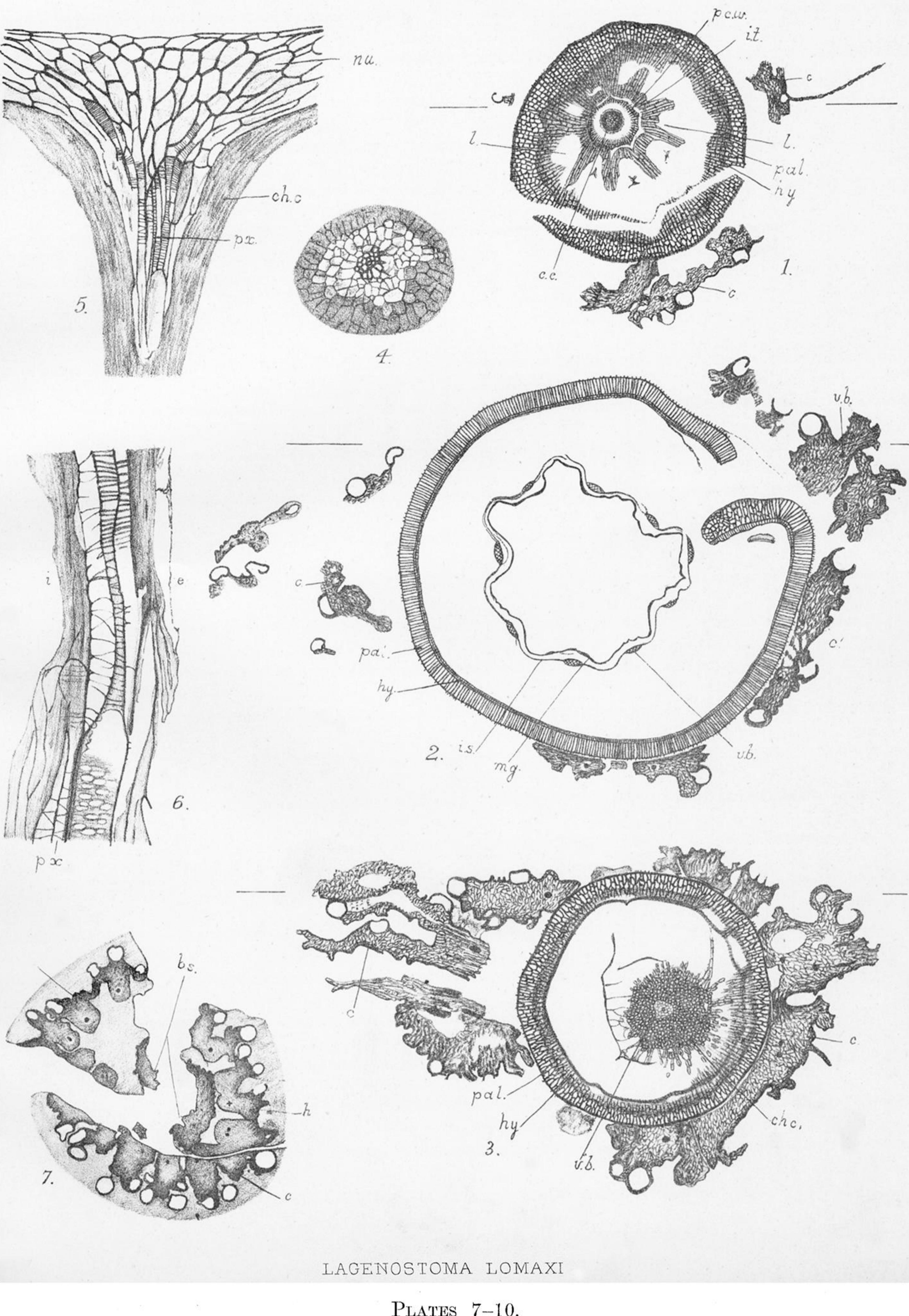
W. 1931, *A.* \times about 80. (See p. 227.)

Phot. 26.—Detached vegetative gland. Here the glandular tissue, *gl. t.*, is breaking down, showing a lenticular gap in the middle.

W. 1931, *A.* \times about 80. (See p. 227.)

Phot. 27.—Vascular bundle, in transverse section, from a small rachis of *Lyginodendron Oldhamium*, to compare with the bundle from the pedicel of the seed shown in Plate 8, fig. 10. Only the xylem is preserved; *px.*, position of median protoxylem group. Lateral protoxylem was no doubt present also, to the right and left.

S. 448. \times about 80. (See pp. 221 and 228.)



LAGENOSTOMA LOMAXI

PLATES 7-10.

Figures from camera lucida drawings. Those in Plates 7 and 8 by Mr. L. A. BOODLE; Plate 10, figs. 27, 28, 28A and B, and 34 by Miss M. C. STOPES; all the other figures by one of the authors.

PLATE 7.

Figs. 1-3.—Series of three approximately transverse sections of the same seed; the orientation of the sections is uniform throughout the series.

Fig. 1.—Uppermost section, passing through the canopy. *c.*, *c.*, portions of the cupule, containing vascular bundles and bearing glands; *pal.*, palisade; *hy.*, hypoderm of testa, cut obliquely; *l.*, *l.*, loculi of the canopy (nine in all), separated by radial septa; *i. t.*, inner wall of canopy; *p. c. w.*, wall of pollen-chamber; *c. c.*, central cone of pollen-chamber.

W. 1915, M. $\times 18\frac{1}{2}$. (See pp. 198, 204, and 218.)

Fig. 2.—Middle section through the body of the seed. *c.*, *c'*, portions of the cupule, of which many fragments are shown; *c'*, the largest continuous piece (a number of glands and vascular bundles are shown); *v. b.*, the bundle represented in fig. 16; *pal.*, palisade; *hy.*, hypoderm of testa; *i. s.*, intermediate sack on which the nine vascular bundles abut; *v. b'*, the bundle represented in Plate 5, phot. 14; *mg.*, membrane of megasporangium.

W. 1915, O. $\times 18\frac{1}{2}$. (See pp. 198 and 218.)

Fig. 3.—Lowest section, through chalaza. *c.*, *c.*, cupule, which is here nearly complete; *pal.*, *hy.*, palisade and hypoderm of testa, cut obliquely; *ch. c.*, chalazal cushion; *v. b.*, vascular bundle of chalaza, shown enlarged in fig. 4.

S. 236. $\times 18\frac{1}{2}$. (See pp. 198 and 218.)

Fig. 4.—Vascular bundle of chalaza and surrounding tissues, transverse section. In the xylem the smallest elements are nearly central (cf. fig. 5). The phloëm is not well defined.

S. 236. $\times 90$. (See pp. 209 and 210.)

Fig. 5.—Vascular bundle and surrounding tissues of chalaza in longitudinal section. *px.*, central protoxylem of bundle; *nu.*, tissue at base of nucellus; *ch. c.*, part of the chalazal cushion (cf. Plate 4, phot. 7).

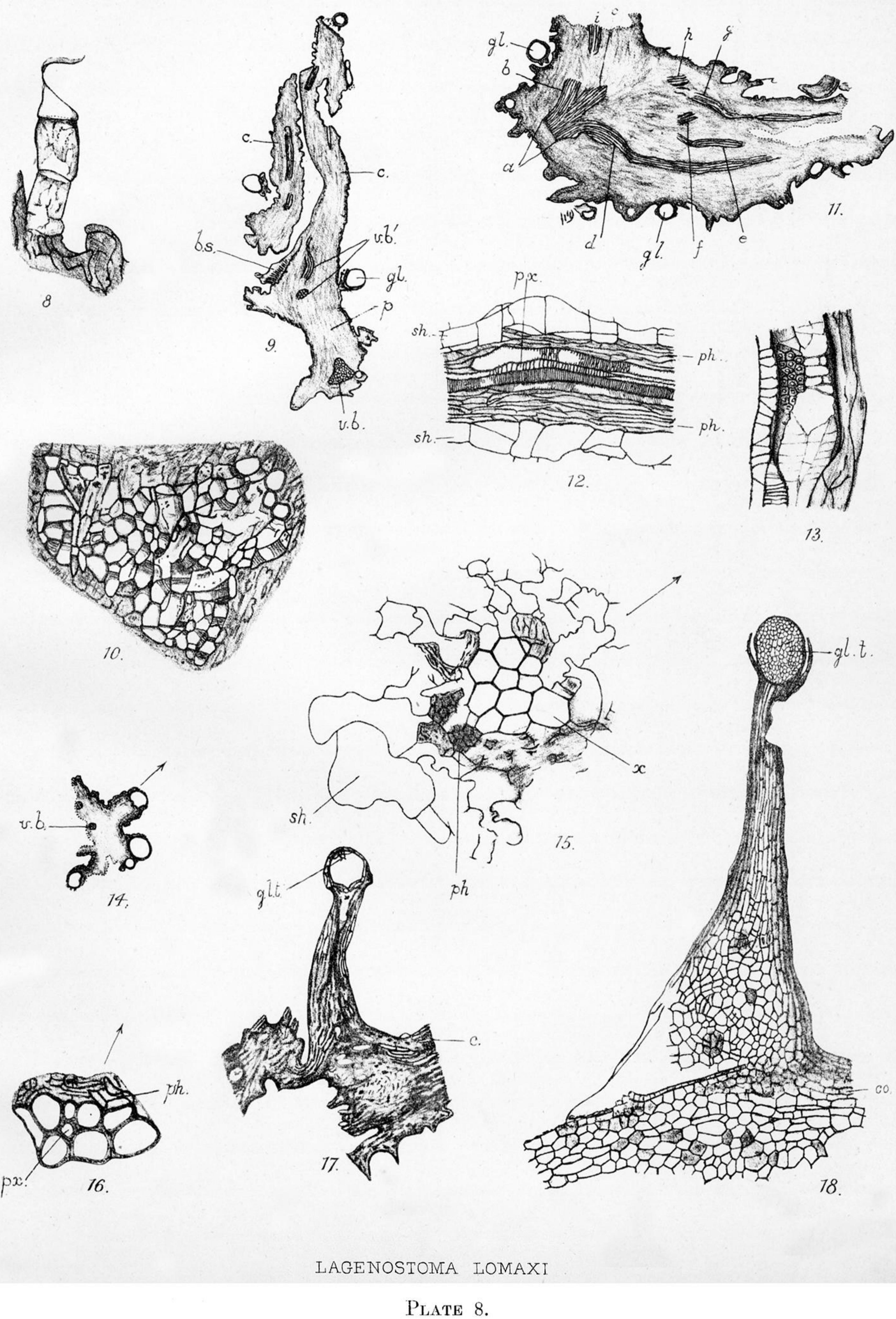
W. 1930. $\times 98$. (See pp. 209 and 210.)

Fig. 6.—Part of a vascular bundle from a full-grown seed, in approximately radial section. *i.*, inner; *o.*, outer side; *px.*, protoxylem element. The other tracheides are spiral or scalariform, and in one case pitted. Some of the narrow elements adjacent to the xylem may be phloëm.

W. 1931, A. $\times 390$. (See p. 210.)

Fig. 7.—Transverse section through the lower part of a cupule, bearing numerous glands and containing vascular bundles. *c.*, *c.*, cupule; *b. s.*, *b. s.*, tissue at base of seed; *h.*, hair represented in fig. 8. The specimen is split into two unequal parts by a wide crack.

Section lent by Miss BENSON. H. 55. $\times 18\frac{1}{2}$. (See p. 217.)



LAGENOSTOMA LOMAXI

PLATE 8.

Fig. 8.—Hair, from the cupule shown in fig. 7.

H. 55. $\times 390$. (See p. 224.)

Fig. 9.—Cupule and pedicel in approximately tangential section. *p.*, pedicel; *c.*, *c.*, cupule, one portion of which is detached; *gl.*, gland *in situ*; *b. s.*, tissue at base of seed, which is lost; *v. b.*, vascular bundle of pedicel, represented enlarged in fig. 10; *v. b'*, bundles passing out into cupule.

U. C. L., R. 15. $\times 18$. (See p. 220.)

Fig. 10.—Vascular bundle of pedicel shown in fig. 9, in somewhat oblique transverse section. Some of the gaps in the wood probably represent position of protoxylem.

U. C. L., R. 15. $\times 175$. (See p. 220.)

Fig. 11.—Cupule, in approximately tangential section, shown also in Plate 6, phot. 17. *a*, vascular bundle of pedicel; *b*, *c*, *d*, *e*, *f*, *g*, *h*, *i*, vascular bundles of cupule; *gl.*, *gl.*, glands.

U. C. L., R. 14, *a.* $\times 18$. (See p. 219.)

Fig. 12.—Part of the vascular bundle marked *e.* in fig. 11, showing xylem with phloëm on each side. *px.*, protoxylem; *ph.*, phloëm; *sh.*, *sh.*, bundle-sheath.

U. C. L., R. 14, *a.* $\times 150$. (See p. 222.)

Fig. 13.—Part of the vascular bundle marked *b.* in fig. 11, showing a large tracheide with multiseriate bordered pits.

U. C. L., R. 14, *a.* $\times 390$. (See p. 222.)

Fig. 14.—Detached portion of cupule, bearing glands. Two vascular bundles are shown; that marked *v. b.* is represented in fig. 15. The arrow has the same direction as in that figure.

U. C. L., R. 14, *a.* $\times 18\frac{1}{2}$. (See p. 222.)

Fig. 15.—The vascular bundle marked *v. b.* in fig. 14. *x.*, the large-celled xylem; *ph.*, phloëm; *sh.*, bundle-sheath. The arrow, as in fig. 14, points outwards, showing that the orientation of the bundle is, in this case, reversed.

U. C. L., R. 14, *a.* $\times 390$. (See p. 222.)

Fig. 16.—Another vascular bundle from a cupule (that marked *v. b.* in fig. 2). *px.*, protoxylem, in the interior of the xylem strand; *ph.*, phloëm. The arrow points outwards (parallel to the axis of the adjacent gland, see fig. 2), and thus the orientation is here normal.

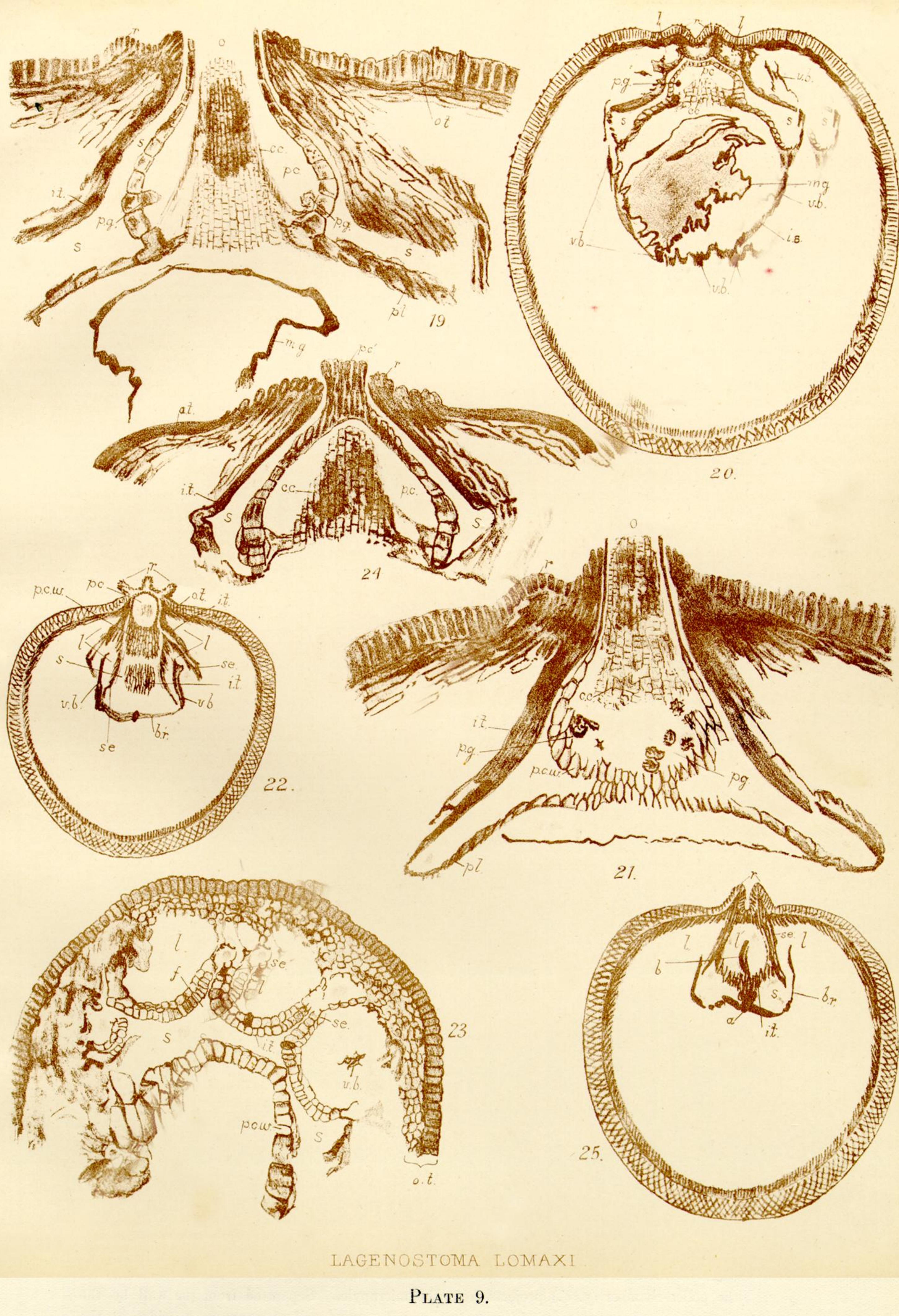
W. 1915, O. $\times 390$. (See p. 222.)

Fig. 17.—Long gland borne on a cupule. *c.*, cupular tissue; *gl. t.*, remains of glandular tissue in cavity of head.

U. C. L., R. 14, *b.* $\times 38$. (See p. 223.)

Fig. 18.—Long gland, borne on a stem of *Lagenostoma Oldhamianum*. *co.*, cortex of stem; *gl. t.*, glandular tissue of the head, perfectly preserved. The peripheral wall of the head is broken at the top.

S. 1781. $\times 38$. (See p. 225.)



LAGENOSTOMA LOMAXI

PLATE 9.

Figs. 19-25, *Lagenostoma Lomaxi*.

Fig. 19.—Nearly median longitudinal section of the pollen-chamber and adjacent parts of a full-sized seed. *p. c.*, cavity of pollen-chamber; *p. g.*, pollen-grain (two are present); *c. c.*, central cone of pollen-chamber; *o.*, orifice of pollen-chamber; *s.*, sinus between canopy and pollen-chamber; *pl.*, plinth supporting the pollen-chamber; *i. t.*, inner wall of canopy or integument; *o. t.*, outer wall of canopy; *r.*, ridge on testa radiating from micropyle. The ridge is cut obliquely, owing to the section being slightly tangential and oblique; *mg.*, crumpled wall of megasporangium.

U. C. L., R. 1. $\times 60$. (See p. 200.)

Fig. 20.—Oblique section of a full-sized seed. The section starts near the micropyle, cutting the two middle loculi of the canopy as it enters almost transversely. It then strikes the pollen-chamber at mid-height, and, sloping down, cuts its base almost at the full diameter; continuing, the section cuts the intermediate sack and megasporangium obliquely and travels out of the seed about two-thirds down the side remote from that at which it entered. *l.*, loculus of canopy; *s.*, septum of canopy (still showing the compressed groove in its median plane); *r.*, ridges on surface overlying the septa of the canopy; *p. c.*, pollen-chamber; *p. g.*, pollen-grain; *c. c.*, central cone of pollen-chamber; *s.*, sinus around plinth and pollen-chamber; *v. b.*, *v. b.*, vascular bundles abutting on the intermediate sack (*i. s.*); *mg.*, megasporangium.

Section lent by Professor F. E. WEISS. Manchester Collection, K₂, 14257. $\times 27$. (See p. 200.)

Fig. 21.—A somewhat tangential section of a pollen-chamber of a full-sized seed. *p. c. w.*, wall of pollen-chamber. Below, in the middle of the figure, just where the pollen-chamber is constricted, a portion of the wall is cut tangentially. *p. g., p. g.*, pollen-grains lying in the cavity of the pollen-chamber (about half a dozen are present); *c. c.*, central cone of tissue; *o.*, orifice of pollen-chamber; *r.*, ridge on outside of canopy, cut obliquely; *i. t.*, inner wall of canopy; *s.*, sinus round pollen-chamber; *pl.*, plinth.

U. C. L., R. 2. $\times 62$. (See p. 200.)

Fig. 22.—Oblique section across the canopy and pollen-chamber of a full-sized seed. The section entered the seed at the very edge of the micropyle, where it cuts three of the ridges (*r. r.*) obliquely. It passes obliquely into the neck of the pollen-chamber (*p. c.*), in leaving which it follows the plane of the wall (*p. c. w.*) for some distance. Below and flanking the pollen-chamber is the gap or sinus (*s.*). Two loculi of the canopy (*l. l.*) are cut into on either side, and the lower pair of loculi show their vascular strands (*v. b., v. b.*) lying in the plane of section. Part of the inner tangential wall of a fifth loculus is seen as an island of tissue (*i. t.*); *se., se.*, septa separating loculi. The transverse bar below these structures is the bundle-ring (*b. r.*). It is continued up on the left side as far as the second septum. The section passes out of the seed a little more than one-third of the way down.

KIDSTON Collection, 260. $\times 20$. (See p. 200.)

Fig. 23.—Transverse section across the canopy and pollen-chamber of a small-sized seed. *p. c. w.*, wall of pollen-chamber, shifted somewhat from its true position. On the left the cells are much displaced; *s.*, sinus; *i. t.*, inner, fluted face of canopy; *f.*, groove on inner face of canopy; *l. l.*, loculi of canopy; *se., se.*, septa—both those shown are double; *v. b.*, vascular bundle lying in a loculus; *o. t.*, outer wall of canopy.

U. C. L. Collection, R. 11. $\times 95$. (See p. 203.)

Fig. 24.—Median longitudinal section of a young abortive seed. The pollen-chamber (*p. c.*) stands in the centre of the figure with its central cone of tissue (*c. c.*) rising from the base. The tube of the pollen-chamber (*p. c.*) projects from the micropyle. Separated from the wall by the sinus (*s.*) is the canopy. *i. t.*, inner wall; *o. t.*, outer wall of canopy; *r.*, ridge at the micropyle. The plinth was undeveloped at this stage of development.

W. 1931, A, small seed. $\times 65$. (See p. 200.)

Fig. 25.—An oblique section across the canopy of a full-sized seed. As in fig. 22, this section enters the seed close to the micropyle cutting across a pair of ridges (*r.*) very obliquely; it then (unlike fig. 22) slopes away from the pollen-chamber, cutting the middle loculus of the canopy (*l.*) parallel to its inner wall. *l. l.*, other loculi of canopy; *a.* and *b.*, vascular bundle cut twice, once below the canopy (*a.*) and again as it runs up the loculus (*b.*); *b. r.*, bundle-ring; *s.*, sinus; *se.*, septum of canopy; *i. t.*, inner wall of canopy. The section leaves the seed about half-way down the same side as that which it entered.

KIDSTON Collection, 424. $\times 21$. (See p. 204.)



LAGENOSTOMA LOMAXI

PLATE 10.

Figs. 26-34, *Lagenostoma Lomaxi*.

Fig. 26.—Slightly oblique longitudinal section of the chalaza of a full-sized seed. *a. l.*, marks the position of the abscission-layer; *ch. c.*, the chalazal cushion; *pal.*, the palisade layer, thinning out at the seed-base; *hy.*, the fibrous hypoderm; *v. b.*, three of the branch vascular strands shown, one in transverse, the other two in somewhat oblique section. The main chalazal bundle does not lie in the plane of section; *nu.*, tissue at base of nucellus.

U. C. L. Collection, R. 4. \times about 60. (See p. 207.)

Fig. 27.—Oblique section through the chalazal region of a full-sized seed. Starting rather near the periphery of the scar and passing upwards and inwards, the section strikes the axis of the seed just at the point of branching of the chalazal bundle. Here the bundle *a* is cut nearly transversely, *b* longitudinally, and *c* obliquely. Three bundles run entirely outside the plane of section, whilst the remaining three, *d*, *e*, and *f*, are cut higher in their course after they have turned the corner of the intermediate sack. *a. l.*, abscission-layer; *ch. c.*, fibres of the chalazal cushion, cut nearly transversely in the lower part of the figure; *nu.*, tissue at base of nucellus; *pal.*, palisade-layer.

Section lent by Professor C. E. BERTRAND, Lille, Lab. Bot. Collection, 1110. \times 43. (See p. 207.)

Figs. 28, 28A, and 28B.—Palisade cells with pegs from full-sized seed.

All from Lille, Bot. Lab. Collection, 1108.

Another section from the seed given in fig. 27.

\times about 180. (See p. 206.)

Fig. 28.—A palisade cell (*pal.*) with peg (*pe.*).

Fig. 28A.—Two palisade cells with pegs. This figure shows the most usual type of preservation.

Fig. 28B.—Several palisade cells with pegs raised to various heights by mucilage cones. *pal.*, palisade cells; *hy.*, hypoderm; *pe.*, *pe.*, pegs; *mu.*, mucilage-cone.

Fig. 29.—Portion of a transverse section of the wall of a full-sized seed from about the middle part of the seed showing a vascular bundle cut *in situ*. *pal.*, palisade-layer; *pe.*, peg; *hy.*, hypoderm, with "thick" preservation; *v. b.*, vascular bundle; *mg.*, megasporangium.

U. C. L. Collection, R. 7, b. \times about 100. (See p. 209.)

Fig. 30.—Portion of a transverse section of a full-sized seed cut at a height corresponding to the insertion of the pollen-chamber. *pal.*, palisade-layer; *o. s.*, outer sack of the seed; *b. r.*, bundle-ring; *v. b.*, vascular bundle; *i. t.*, internal wall of canopy.

U. C. L. Collection, R. 6, c. \times 32. (See p. 203.)

Fig. 31.—Portion of intermediate sack (*i. s.*) from a transverse section cut half-way up the same seed. The bundles, *v. b.*, *v. b.*, are connected, as usual, by the bundle-ring (*b. r.*), from which at places an inner ring (*i. r.*) has separated; *mg.*, megasporangium. (*b. r.* + *i. r.* = *i. s.*)

U. C. L. Collection, R. 6, b. \times 60. (See p. 202.)

Fig. 32.—Papillae from a ridge near the micropyle of a small seed.

W. 1931, A. (small seed). \times about 400. (See p. 206.)

Fig. 33.—Longitudinal section through a full-sized seed showing continuity of seed-base with the pedicel and insertion of the cupule. *p.*, pedicel; *v. b.*, vascular bundle of pedicel; *c.*, *c.*, cupule; *gl.*, *gl.*, glands on pedicel and cupule; *a. l.*, abscission-layer; *ch. c.*, chalazal cushion; *pal.*, palisade-layer. See also photos. 15 and 16.

S. 558. \times about 15. (See p. 217.)

Fig. 34.—Median longitudinal section of a young seed or ovule, showing continuity of seed, pedicel, and cupule. The irregular black, knob-like layer is the surface of the testa, curiously preserved. The black pipes in the interior of the seed represent sections of the collapsed and folded megasporangium and nucellus. *p.*, pedicel; *c.*, *c.*, cupule; *c.*, long lobe of cupule; *gl.*, *gl.*, glands; *h.*, tuft of uniseriate hairs on long lobe of cupule; *ch.*, chalaza, somewhat above position of abscission-layer; *pal.*, young palisade-layer; *i. s.*, collapsed megasporangium and nucellus; *p. c. w.*, pollen-chamber wall; *c.*, *c.*, central cone of pollen-chamber; *o.*, orifice of pollen-chamber; *s.*, sinus; *v. b.*, *v. b.*, vascular bundles; *a.*, point of insertion of bundle to cupule.

U. C. L. Collection, R. 13. \times about 33. (See p. 213.)